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16 ABSTRACT

A research program was initiated to understand the dynamics of a relatively undisturbed estuary-marshland ecosystem, the North Inlet Estuary near Georgetown, South Carolina. Because of the relative complexity of this type of study, a five year study was proposed; this report summarizes results of the first two years.

This study consisted of two substudies: a macroecosystem substudy and a microecosystem substudy. The objectives of the macroecosystem study were: 1) to establish baseline data on an undisturbed estuary to provide a scientific basis for comparative studies on effects of various stresses of pollutants on other estuarine environments; and (2) to develop models of an estuarine ecosystem which would predict probable effects of environmental perturbation. The principal objective of the microecosystem study was to develop and test replicate experimental salt marsh units at the microecosystem level as diagnostic tools for the assessment of both long- and short-term pollution effects on the Spartina alterniflora salt marsh community.

A conceptual model of energy flow for the entire marsh-estuarine ecosystem was developed which consisted of three sub-models. A simulation of the water column sub-model and a simulation by a linear systems model of an intertidal oyster community was completed. Much baseline data needed for model development is available on primary producers, zooplankton, meiofauna, benthic macrofauna, decomposers, and relevant physical parameters.

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THE DYNAMICS OF AN ESTUARY

AS A NATURAL ECOSYSTEM

by

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FOREWORD

To evaluate effects of pollution on estuarine populations, communities, and ecosystems, it is necessary to understand their structures and functions under natural, unstressed conditions. Without an understanding of normal situations, it would be difficult for the Environmental Protection Agency to carry out its mission in the fields of surveillance and regulation. The Environmental Research Laboratory, Gulf Breeze conducts field research programs in an effort to learn natural conditions in estuarine ecosystems on the eastern and Gulf coasts of the United States.

This report describes ecological research that was done in a two-year period in a relatively unpolluted salt-marsh ecosystem on the eastern seaboard. It also describes uses of an artificial salt-marsh ecosystem for study of aspects that cannot be studied in the field. The data are being used for construction of mathematical and conceptual models that describe physical, chemical, and biological aspects of the marsh. The models will be published in an EPA Ecological Series Report.

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ABSTRACT

Although estuaries and marshlands are valuable as a natural resource, integrative scientific studies leading to the development of predictive models are practically nonexistent. Such studies are necessary for effective pollution control and long-term management of the estuarine ecosystem.

A research program was initiated to understand the dynamics of a relatively undisturbed estuary-marshland ecosystem, the North Inlet Estuary, near Georgetown, South Carolina. Because of the relative complexity of this type of study, a five year study was proposed; this report summarizes results of the first two years.

This study consisted of two separate but interrelated substudies: a macroecosystem substudy and a microecosystem substudy. The objectives of the macroecosystem study were: 1) to establish baseline data on an undisturbed estuary to provide a scientific basis for comparative studies on effects of various stresses of pollutants on other estuarine environments; and 2) to develop models of an estuarine ecosystem which would predict probable effects of environmental perturbation. The principal objective of the microecosystem study was to develop and test replicate experimental salt marsh units at the microecosystem level as diagnostic tools for the assessment of both long- and short-term pollution effects on the Spartina alterniflora salt marsh community.

A conceptual model of energy flow for the entire marsh-estuarine ecosystem was developed which consisted of three sub-models. A simulation of the water column submodel and a simulation by a linear systems model of an intertidal oyster community was completed. Much baseline data needed for model development is available on primary producers, zooplankton, meiofauna, benthic macrofauna, decomposers, and relevant physical parameters. An interdisciplinary team of marine scientists has developed the capability to work together to solve a common complex problem. This five year study was designed to be developed in specific phases. Modeling, field work, and an experimental approach were developed simultaneously. However, the additional phases need to be studied in order to complete the initial objectives.

This report was submitted in fulfillment of Grant No. R 802328 by the University of South Carolina, P. John Vernberg, principal investigator, under the sponsorship of the U.S. Environmental Protection Agency. This report covers a period from January 14, 1974 to January 13, 1976 and work was completed January 13, 1976.

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SECTION I

INTRODUCTION

The value of marshlands and estuaries to man as natural resources is indisputable and has been stressed by numerous national reports. Estuaries and their surrounding marshlands have served as centers of population and are heavily utilized for industrial development, shipping, fishing, and recreation. Furthermore, such usage is destined to increase in the future, with the predictable result of increased competition for these limited natural resources. Estuaries have been exploited to varying degrees; in some, almost the total biota have been ruined. Despite recognition that estuaries are not an unlimited resource, integrated scientific studies leading to the development of predictive models are practically non-existent. Such integrated studies, rather than isolated studies of individual species, are necessary for effective pollution control and long-term management of the estuarine ecosystem. In particular, production, energetics, and the mechanisms of various processes as influenced by environmental perturbation are poorly understood, although the knowledge of these factors has obvious economic and fundamental scientific values.

Great diversity in kinds and shapes of estuaries has been reported in the scientific literature (Lauff, 1967; Odum et al., 1974). However, estuaries typically have certain characteristics in common, such as tidal fluctuation, salinity changes, and high concentrations of nutrients. Differences between estuaries may be quantitative or qualitative, such as the amount of wetlands or the amount and types of human habitation bordering their shores. Therefore, it is important to develop and compare ecosystem-oriented models of the major estuarine types if we are to assess the universal nature and differences of estuarine dynamics.

This study was undertaken to understand the ecosystem dynamics of a relatively undisturbed estuary, the North Inlet Estuary near Georgetown, South Carolina. This report describes the initial two-year study of what was designed to be a five-year project. After the project began, the study was expanded to include a specific section on a microecosystem.

This study consisted of two separate but interrelated substudies, that of the macroecosystem, and that of the microecosystem. For purposes of clarity, objectives are presented separately.

MACROECOSYSTEM STUDY

This was designed to study the dynamics of a relatively undisturbed marsh-estuarine ecosystem. There were two interrelated objectives of this study: 1) to establish baseline data on an undisturbed estuary to provide a scientific basis for comparative studies on effects of various stresses of pollutants on other estuarine environments; and 2) to develop models of an estuarine ecosystem which would predict probable effects of environmental perturbation.

MICROECOSYSTEM STUDY

The prime objective was to develop and test replicate experimental salt marsh units at the microecosystem level as diagnostic tools for the assessment of both long- and short-term pollution effects on the Spartina alterniflora salt marsh community.

Results of this integrated study add significantly to our understanding of the marsh-estuarine ecosystem. Not only does this study provide better insight into the functioning of estuarine processes in an undisturbed estuary, but it also provides a basis for the development and validation of the predictive models. These models are needed in making decisions on environmental impact of man's activities in the estuarine environment and in developing long-term management programs of this vital natural area.

SECTION 8

CONCLUSIONS

Results in the first two years of a proposed five-year analysis of a relatively undisturbed marsh-estuarine ecosystem and a salt marsh microcosm system program have resulted in development of a conceptual model of energy flow, a simulation of the water column submodel, and simulation by a linear systems model of an intertidal oyster community. Much baseline data needed for model development is available on primary producers, zooplankton, meiofauna, benthic macrofauna, decomposers, and relevant physical parameters. An interdisciplinary team of marine scientists has developed the capability to work together to solve a common complex problem. This five-year study was designed to be developed in specific phases. Modeling, field work, and an experimental approach were developed simultaneously. However, the additional phases need to be studied in order to complete the initial objectives.

SECTION 3

RECOMMENDATIONS

Since this two-year project was designed as the initial phase of a five-year project, definitive recommendations are premature. However, we suggest:

1) The study of relatively undisturbed ecosystems is necessary to understand the dynamics of how systems work and to serve as a vital baseline with which to compare perturbed areas.

2) Since natural environmental units are complex and it takes time and effort to analyze them, it is recommended that granting agencies recognize the need for supporting long-term projects. To develop an interdisciplinary team, such as involved with the North Inlet Estuarine Study, is difficult and once assembled it should be allowed to accomplish its initial goals.

SECTION 4

REVIEW OF PERTINENT ESTUARINE ECOSYSTEM STUDIES

One of the first attempts to construct an energy flow diagram for an estuarine-marsh ecosystem was that of Teal (1962) for the marshes of Sapelo Island, Georgia. Teal proposed an energy flow diagram based on the data of various investigators. During a year the input of solar energy was 600,000 kcal/m^2. This energy was estimated to be partitioned as follows: most of the energy (93.9%) was lost in photosynthetic activity, gross production was 6.1%, and net production was about 1.4% of the incident light energy. Of the energy available to secondary consumers, 55% was expended in respiration, while 45% of net production was exported. Since this study, more detailed energy budgets have been published for various individual species found in the estuarine-marsh ecosystem (Odum, 1971; Hughes, 1970) and other estuarine systems have been studied as described below.

Recently, a detailed study of a New England salt marsh was made by Nixon and Oviatt (1973). The two studies differed in that Teal emphasized energy flow in the marsh, while Nixon and Oviatt were concerned with energy flow in marsh creeks and embayments. Since consumption for the embayment exceeded production based on a yearly energy budget, this aquatic system must depend on input of energy in the form of organic detritus from marsh grasses. Production values of New England marsh grass were similar to those from New York, but markedly lower than those of southern marshes. This finding may reflect the substantial difference in climatic conditions between these geographical regions. Marked seasonal differences in energy flow patterns of New England ecosystems were observed. The flow of energy is much more complex and values are higher during summer than in winter. Thus, pollutants introduced at different times of the year might not only have a greater differential seasonal effect on northern marshes, but northern marshes might respond differently than those in southern regions.

To the south, the Newport River estuarine ecosystem is being studied by the Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, Beaufort, North Carolina. Much of this work is reported in the numerous papers of Williams and co-workers (Ferguson and Murdoch, 1973; Thayer, 1971; Thayer et al., 1974, 1975; Williams, 1966, 1973; Williams and Murdoch, 1966) beginning about 1965 and in the annual reports of the United States National Marine Fisheries Service Laboratory, Beaufort, North Carolina. Recently this group reported on the interaction between major plant producers and epifaunal and infaunal invertebrates and fish populations comprising the saltgrass community, a part of the estuarine system not discussed by Teal or

Nixon and Oviatt. Unlike the system studied by Nixon and Oviatt, there appears to be excess food energy for the consumers. Failure of the herbivores and detritivores to expand to the limits of their food reserves suggests that the organisms may be predator-limited: fishes, and shore birds being the primary predators (Thayer, Adams, and LaCroix, 1975). These authors suggest that the excess plant production in the system is likely exported to the adjoining estuary, thus providing food energy, in the form of detritus, to that system. This ecosystem research program also includes detrital cycles, microbial activity studies, export of materials from grass beds, and trace metal studies.

An active program involving Georgia salt marshes has continued since the earlier work of Teal (1962), and recently Wiegert et al. (1975), presented a preliminary ecosystem model of a coastal Georgia Spartina marsh. D.W.L. Pomeroy et al. are continuing studies on the intermediary metabolism of a salt marsh.

The dynamics of energy flow expressed as carbon in an estuarine-marsh ecosystem, Barataria Bay, Louisiana, was described by Day et al. (1973). This study differs from the ones described above in that it deals in greater detail with all parts of the estuarine-marsh complex. Like other marshes, energy was available to be exported to the water, but unlike the findings of Nixon and Oviatt, a net community production in the water column was reported.

Models of larger systems that include estuaries and wetlands as subunits have been developed. One example is that of Young et al. (1974) which uses models of energy relationships on a regional basis to develop a management plan for development and channelization of the Atchafalaya Basin of Louisiana.

In January 1976 an ecosystem study of a relatively undisturbed estuary, the North Inlet Estuary, Georgetown, South Carolina, was formally initiated by the Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina with support from the Environmental Protection Agency. The North Inlet Estuary is unique in the United States in that it is sufficiently large to have estuarine characteristics and at the same time it is sufficiently small to be studied comprehensively. Furthermore, and of great importance, most of the water and tidelands associated with this estuary and the adjacent undeveloped highlands are within the property boundaries of a private Foundation, the Belle W. Baruch Foundation. The Foundation has as one of its stated goals the long-term preservation of this natural area. Hence this area is ideally situated for long-term study of marsh-estuarine processes.

Our study differs from those on other southeastern estuaries in that the North Inlet Estuary is relatively simple and discrete, representing a different type of estuarine system. For example, in North Carolina the Newport River Estuary represents a large, complex system bordered by industries and human habitation, while the marshes of Sapelo Island, Georgia are a small part of a large bay system encompassing numerous islands. Our study represents a comprehensive, interdisciplinary study involving a number of investigators working simultaneously to understand complex estuarine processes. In

this manner data collection for various discrete but interacting processes can be collected at one time, thus providing a comparable data base for interpretation of how these processes function. Some other models have suffered because the best available data were collected either in distantly located estuaries or in the same estuary but in different years and for different purposes.

Because of the complex nature of this study, which directly involved ten faculty members and two post-doctoral investigators and indirectly a number of other faculty who were studying related projects funded through other sources, this report is presented in the following format:

1. Study site description
2. Overview, including a general discussion of the plan of study involving the various substudies
3. Substudies, including a detailed analysis of the various interrelated parts of the energy flow model
4. Summary of entire study

SECTION 3

STUDY SITE DESCRIPTION

The Belle W. Baruch Foundation property referred to as the Hobcaw Barony is located near Georgetown, South Carolina (Fig. 1). It is unique along the eastern coast of the United States for marsh-estuarine studies for the following reasons:

1. The North Inlet Estuary and marshlands are chiefly confined within the property lines of the Belle W. Baruch Foundation (Fig. 2). The Foundation is dedicated to conservational research and has established its lands and marshes for long-term studies in marine science.

2. The estuary and marshlands are relatively undisturbed. Their waters are classified by the South Carolina Department of Health and Environmental Control as "highest quality." The estuary is sufficiently small to be studied in detail, but large enough to have distinctive estuarine characteristics. The inlet is approximately 0.88 km wide and the distance from the inlet to the pier at Clambank is approximately 3.06 km by boat. The total estuarine and tideland areas cover an area of approximately 28.06 km^2.

3. The marshlands and estuary are sufficiently large to permit experimental manipulation and control of experimental areas, and extensive land holdings provide space for construction of experimental ponds. Extensive oyster beds are found in this region as well as large populations of other commercially important species, such as blue crab, shrimp, and mullet.

4. Study of the biota and physical parameters of the marshes and estuary has been in progress since January 1970. Although far from being a complete study, data from these investigations furnish a realistic basis for future studies.

5. The present staff of 32 associates of the Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, has demonstrated its ability to work on complex problems in a coordinated manner.

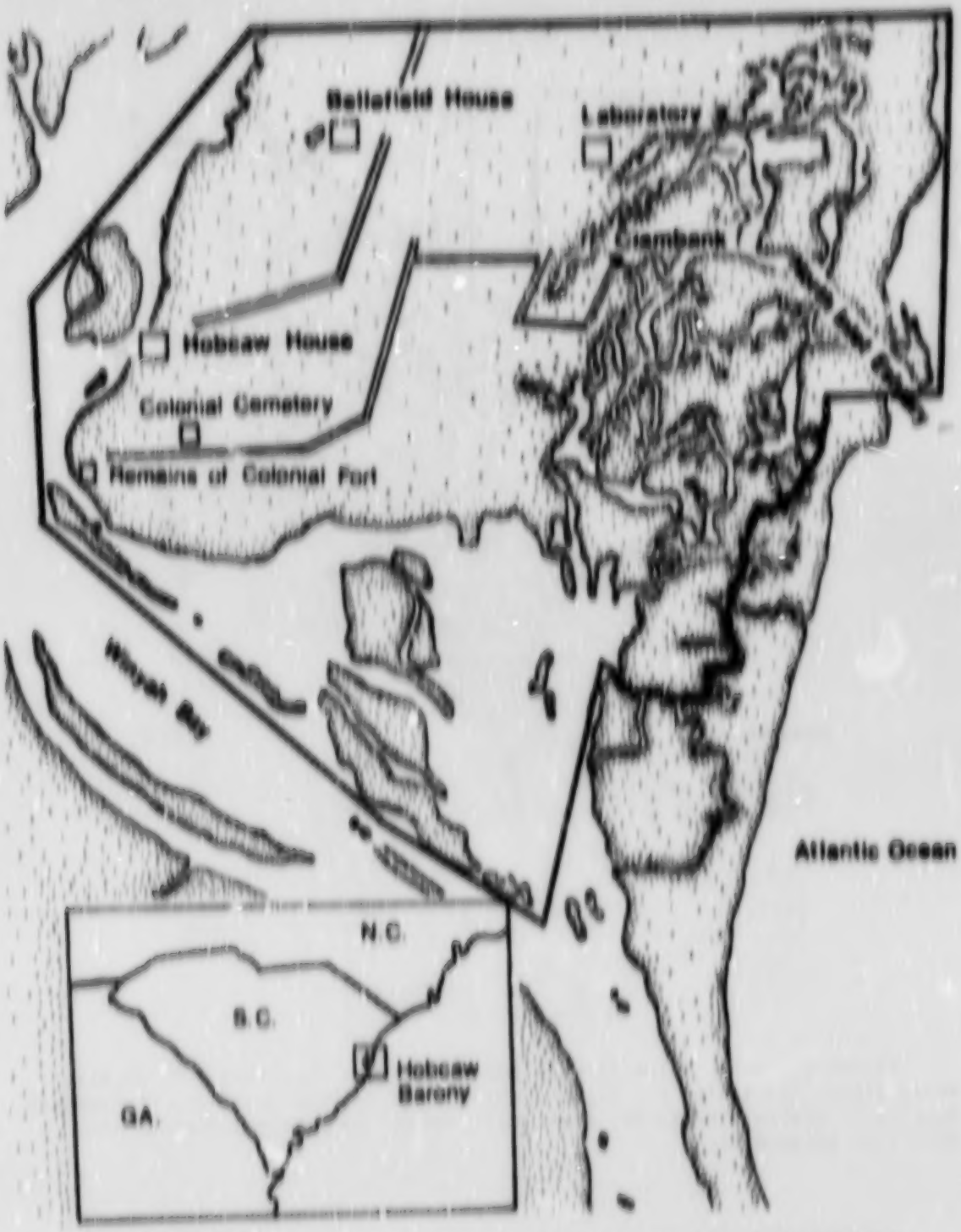

Figure 1. The Hobcaw Barony, Property of the Bella W. Baruch Foundation.

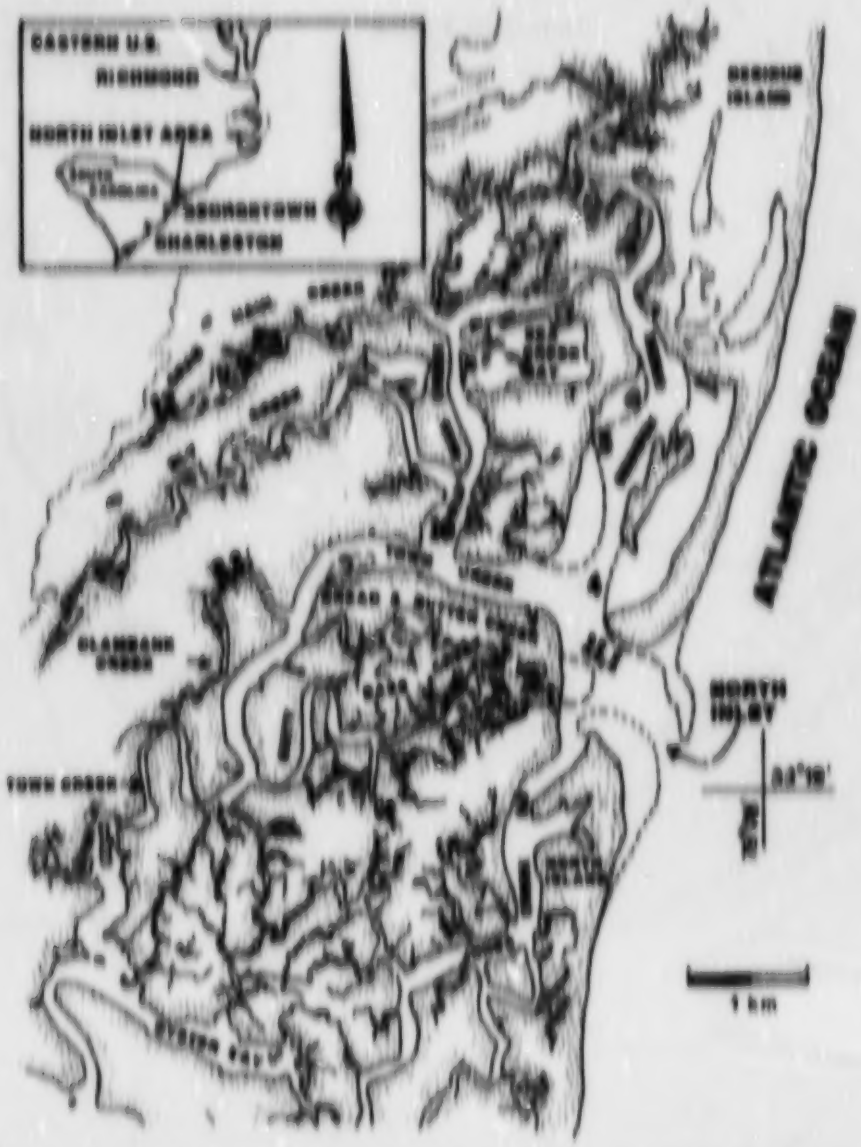

Figure 2. North Inlet Estuary and marshlands. Stations 1-5: Dr. Dame's study sites; Station 6: Dr. Stevenson's Station 1; station 7: Dr. Stevenson's Station 2; Stations 8-11: Dr. Stevenson's other study sites; Station 12: Radiation balance site.

GEOLOGIC SETTING

North Inlet waters drain a very large marsh located between Debidue Beach and North Island and the mainland. The mainland consists of Pleistocene Storm Beach Terrain with ridges oriented in a northeasterly-southwesterly direction. These ridges intersect the Atlantic Ocean at the north end of Debidue Beach. These surficial mainland features are underlain by a complex sequence of older coastal plain sediments, a sequence which is poorly understood in the immediate area at the present time.

Debidue Beach and North Island represent part of a Holocene Barrier Beach System. This system has migrated southward in recent times, with principal evidence here being the major spit along the northern entrance to Winyah Bay, and smaller spit migration land forms along the northern border of North Inlet.

North Inlet drains numerous tidal creeks and two of these extend back through the marsh to lie in close proximity to the Pleistocene mainland. The creeks are very shallow, never exceeding 9.12 m below mean sea level and commonly show floors which are occupied by sand bars. The marsh areas are underlaid by silts and clays which extend to an unknown depth.

HABITAT TYPES

There is a number of distinctive habitat types within the North Inlet Estuary. There are approximately 2,630 ha (6,500 acres) of marshland dominated chiefly by Spartina alterniflora. Creek bottoms show, in addition to the sands mentioned above, sandy mud and firm shell substrates. The substrate of the intertidal zone habitats is also variable. Oyster beds and reefs are numerous and extensive; other intertidal zone habitats include open sandy beaches, protected sandy beaches, mud flats showing varying admixtures of sand-sized particles, dunes and forest-marsh edge habitats.

Marked seasonal changes in temperature have been recorded; air temperatures range from about -10°C to above 33°C; water temperatures range from 9°C to approximately 32°C. The salinity may range from about 10 °/oo to above 35 °/oo. Typically, the salinity is 30 °/oo or higher. Tidal amplitude is about 1.82 m.

SECTION 6

OVERALL VIEW

Since estuarine processes are complex, it is recognized that the development of comprehensive estuarine models will take time. The early phase of this program included development of an energy flow conceptual model of the North Inlet Estuary. Baseline data were collected on some of the major components, but not all compartments of the model were studied initially. Where possible, data from published studies of other estuarine and marshes were used in model development.

Three major aspects of the estuarine-marsh ecosystem were studied: 1) structural component; 2) functional processes; and 3) synthetic aspects and modelling. Listed below are the major features of each of these subdivisions and the name of the investigator studying this feature.

A. Structural Components
  1. Biotic factors (Staff)
    a. Communities
      1) Spartina marsh
      2) Oyster, both subtidal and intertidal
      3) Sand beaches, including open and protected sand bars and dunes
      4) Benthic, including the channel bottoms
      5) Plankton
    b. Descriptive aspects of each community
      1) Qualitative and quantitative analysis of species composition
      2) Temporal relationship of community structure
      3) Inter-community comparison of species diversity
    c. Specific groups of organisms
      1) Bacteria - Stevenson
      2) Fungi - Cowley
      3) Algae - Zingmark
      4) Vascular plants - Staff
      5) Meiofauna - Coull
      6) Zooplankton - W. Vernberg, Coull, and DeCoursey
      7) Macro-invertebrates - J. Vernberg and Dame
      8) Fish - Dean
      9) Birds - DeCoursey

  2. Abiotic factors
    a. Sediment (substrate study only) (Colquhoun and Nelson)
      1) Source, type, and chemistry of sediments
      2) Structural features, physical and biotic features

3) Geometry of substrate masses, including marsh, estuarine landforms, barrier islands, bars, and the shelf
4) Accumulation rate

b. Water chemistry (Gardner)
1) Chemistry of interstitial water and the water column
2) Interaction between interstitial and column water

c. Hydrology (Kjerfve)
1) Water mass movements
2) Tidal fluctuations
3) Mixing of water masses
4) Temperature
5) Miscellaneous factors, microenvironmental measurements

d. Measurements of environmental factors (Staff)

B. Functional Processes and Environmental Adaptation

1. Ecological energetics

a. Primary producers
1) Algae (Zingmark)
2) Vascular plants (Staff)

b. Consumers
1) Meiofauna and zooplankton (M. Vernberg, Gouli, and DeCoursey)
2) Energetics of prominent marsh and estuarine macrofauna (J. Vernberg, Dame, Dean, and DeCoursey)

c. Decomposers
1) Environmental effects and the role of heterotrophic bacteria (Stevenson)
2) Fungi as decomposers (Cowley)

2. Nutrient cycling (Kitchens)
3. Role of detritus (Stevenson and Gouli)
4. Export-import dynamics (Kitchens, Kjerfve, and Staff)

C. Synthetic Aspects and Modelling
Model development includes instantaneous and temporal aspects of an estuarine ecosystem (Bonnell and Dame)

Each investigator has written a detailed report which describes his(her) initial phase of what was designed to be a five-year study. The first report by Professor Bonnell describes the energy flow model which was developed by all of the investigators and serves as the unifying framework of the entire study. Within the framework of the overall model, Dr. Dame developed a submodel on the intertidal oyster community. The remaining subetudies deal with various compartments of the energy flow model. The final subetudy deals with the salt marsh microecosystem.

SECTION 7

SUBSYSTEMS

SIMULATION MODEL FOR NORTH INLET ESTUARY

Ronald D. Hunsaki

A comprehensive conceptual energy flow model has been formulated in order to represent the dynamics of North Inlet Estuary. A functional unit with recognizable boundaries and large enough to contain a full set of estuarine ecosystem processes and their interactions was chosen (Fig. 3). The conceptual model has three distinct subsystems:

1) Water Column. The aqueous environment above the benthic subtidal and intertidal marsh zones. Its uppermost boundary is the air-water interface.

2) Intertidal Marsh Zone. The lower boundary of this zone is defined as that portion of the benthic region extending landward from the lower limit of the distribution of creek bank oysters (Crassostrea virginica), siphon tubes of the stout razor clam (Tagelus plebeius) and immediately above the upper limit of the normal distribution of the fire sponge (Microciona prolifera) and the sea pansy (Renilla reniformis). The upper boundary is the upper limit of the vegetational assemblage associated with the high tide mark. This is characterized by the presence of the following species of plants: Spartina alterniflora, S. patens, S. cynosuroides, Juncus roemerianus, Distichlis spicata, Salicornia spp., and/or Iva frutescens.

3) Benthic Subtidal Zone. The area beneath the water column and seaward of the lower limit of the intertidal marsh. Included in the benthic subtidal zone is the material between the sediment-water interface to a depth of 50 cm.

A linear dynamic system with twenty-two states was chosen as the mathematical model for the system, i.e., $\dot{\underline{x}} = \underline{\underline{A}}\,\underline{x} + \underline{\underline{B}}\,\underline{u}$, where

$\underline{\underline{A}}$ = (22 x 22) system matrix
$\underline{\underline{B}}$ = (22 x m) input matrix
$\underline{x}(t)$ = (22 x 1) state vector
$\underline{u}(t)$ = (m x 1) input vector

(t = time; m = number of inputs in the input vector)

Figure 3. North Inlet estuarine ecosystem.

The definitions of the states of the system are given in Table 1. These states represent the variables which the study team determined were most important and are included in the ecosystem model.

The relation matrix for the conceptual model is given in Fig. 4. The high degree of connectivity (approximately 40%) between the states provides an indication of the complexity of the ecosystem. For example, the system matrix $\underline{A}$, alone has approximately 190 coefficients that must be evaluated.

The conceptual model serves as a framework for combining individual studies within the ecosystem and can be used to define the scope of the overall program.

WATER COLUMN SUBMODEL

The water column submodel consists of states X_{16} through X_{22}. All flows of energy into the states of the submodel from other states in the overall model are considered imports, while all flows of energy from the states in the submodel to other states in the overall model are considered exports. Other inputs and outputs to the water column submodel are phytoplankton primary production and respiration of the biotic states and tidal washout. A compartment model illustrating the interaction between the states of the water column submodel and all inputs, outputs, imports and exports is given in Fig. 5.

Several observations can be made concerning the system depicted in Fig. 5. The states X_{18}, X_{19}, and X_{20}, corresponding to herbivores, omnivores, and carnivores respectively, are assumed to be decomposed in the benthic subtidal and not in the water column. Hence, there are no directed branches from these three states to the decomposers in the water column state, X_{21}. Further, the internal self-loops within the compartments for states X_{19} and X_{20} illustrate only that in our grouping of species of omnivores and carnivores, some species of carnivores feed on other carnivores, etc. However, the total energy associated with the state X_{20} is not affected by the internal self-loop. Finally, the input to state X_{16}, $F_{0,16}$, is the energy associated with primary production of phytoplankton and not solar insolation.

Standing Crop Values for Water Column Submodel

The average standing crops over one year for states X_{16} through X_{22} are given in Table 3. These values were computed from actual field data for the year June 1974 through May 1975. Monthly data for the standing crop values of the states are also available and can be used to validate the water column submodel with time-varying system parameter, i.e. $A(t)$ and $B(t)$. However, at present, the time-varying rate parameters have not been evaluated.

System Differential Equations for the Water Column Submodel

The system differential equations for the seven states X_{16} through X_{22} are given in Table 3. Each differential equation was derived by using the conservation of energy principle for each compartment. The linear flows were assumed to be donor controlled, i.e., if a flow of energy, F_{ij}, from state X_j to state X_i occurs, then $F_{ij} = \lambda_{ij} X_j$ where λ_{ij} is the rate constant. Moreover, $1/\lambda_{ij}$ is the turn-over rate for the flow F_{ij} and state X_j.

Import I_{ij} and export E_{ij} are assumed to be constants in the submodel. For each state, import I_{ij} was evaluated by the study team and the export E_{ij} was determined by invoking the steady-state average condition $\dot{X}_i = 0$, and solving for E_{ij}. The value of respiration R_i is included in E_{ij}. A signal flow graph for the water column submodel is given in Figure 6. From the flow graph it is clear that the D.O.M. state X_{22} served as the "sink" for the energy in the water column submodel. Also of interest is the outer loop which encloses all states, the feedback of D.O.M. energy X_{22} to energy associated with phytoplankton X_{16}.

TABLE 1. DEFINITION OF STATE VARIABLES.
All units are expressed as kcal/m^2.

X_1 - Benthic macroflora. The energy associated with those macroscopic algae, including filamentous forms, that are attached to a substrate, but excluding those species of blue-green algae that form mats and that contribute to the stability of the benthic sediments. Primary forms: green, red and brown algae.

X_2 - Benthic microflora. The energy associated with those microscopic algae, both unicellular and multicellular, that are primarily associated with the upper 1-cm of the marsh mud and sand surfaces, including blue-green algae that form mats and contribute to the stability of benthic sediments. Primary forms: diatoms and blue-green algae.

X_3 - Detritus-Benthic subtidal. The energy associated with dead organic material in or on the bottom below mean low tide, including dissolved organic carbon in the sediment.

X_4 - Decomposers-Benthic subtidal. The total microbial biomass (mgC/m^2). Unit measured was ATP. Luciferin/luciferase and biomass carbon were calculated using a conversion factor of 250 mgC per 1 mg ATP (method of Holm-Hansen and Booth, 1966). The biomass of the decomposers (mgC/m^2) was converted to energy (kcal/m^2) by literature values to obtain the energy associated with decomposers-benthic subtidal. The genera of bacteria (decomposers) are: Pseudomonas, Vibrio, Achromobacter, Aeromonas, and Cytophaga.

X_5 - Meiofauna-Benthic subtidal. The energy associated with those benthic animals living below the mean low tide that pass through a 0.5-mm sieve and are retained on a 0.063-mm sieve.

X_6 - Macrofauna-Benthic subtidal. The energy associated with those benthic animals living below the mean low tide that are retained on a 0.5-mm sieve.

X_7 - Grasses. The energy associated with all rooted vegetation growing in the intertidal marsh zone. The dominant species are: Spartina alterniflora, S. patens, S. cynosuroides, Juncus roemerianus, Distichlis spicata, Salicornia virginica, Salicornia sp., Iva frutescens, and Aestrichis frutescens.

X_8 - Detritus-Intertidal. The energy associated with the plant and animal (biogenic) material decomposing in the intertidal marsh.

X_9 - Insects, Snails, etc.-Intertidal. The energy associated with intertidal macrofauna larger than 1-mm mesh which consume plant or detrital material.

X_{10} - Birds. The energy associated with all avian species, both resident and transient, that feed in the intertidal marsh or in the water

Table 1. continued

column. The dominant forms feeding in the water column are: Black Skimmer, terns, Bay and Sea Ducks, pelican, and ospreys. In the intertidal marsh: Marsh Wren, rails, Seaside and Sharp-tailed Sparrows.

E_{11} - Meiofauna-Intertidal. The energy associated with those benthic animals living between mean low water and mean high water that pass through a 0.5-mm sieve and are retained on a 0.063-mm sieve.

E_{12} - Mud crabs-Intertidal. The energy associated with crabs, chiefly Panopeus, Eurypanopeus, and occasionally Uca, which feed upon other animals.

E_{13} - Decomposers-Intertidal. The total microbial biomass in intertidal sediment (reported as mgC/m^2) measured using ATP techniques. Basic measurement is ATP (luciferin/luciferase) and biomass carbon is calculated using the conversion factor of 250 mgC per 1 mg ATP (method of Holm-Hansen and Booth, 1966). The biomass of the decomposers-intertidal (mgC/m^{-2}) is converted to energy ($kcal/m^2$) by literature values to obtain the energy associated with decomposers. The dominant genera of bacteria (decomposers) are: Pseudomonas, Vibrio, Achromobacter, Aerococcus, and Cytophaga.

E_{14} - Oysters, Mussels-Intertidal. The energy associated with the intertidal macrofauna which filter microscopic plant, animal, and detrital material out of the water (filter feeders).

E_{15} - Mammals. The energy associated with all mammal species (exclusive of man) that feed in the intertidal marsh. The dominant forms are: raccoon, otter, feral pigs, Norway Rat, Rice Rat, Cotton Rat, Harvest Mouse, House Mouse, and Deermouse.

E_{16} - Phytoplankton. The energy associated with those microscopic algae, both unicellular and multicellular, that are primarily free-floating in the water column. Primary forms are: diatoms, dinoflagellates, and chrysoflagellates.

E_{17} - Detritus-Water Column. Biogenic particulate organic matter suspended in the water column. The material retained on micro-fine glass fiber filters (Whatman GF/C) and converted to CO_2 by combustion at 500°C.

E_{18} - Herbivores-Water Column. The energy associated with those free-floating or swimming animals that eat living plant material. Primarily the zooplankton but may include some fishes.

E_{19} - Omnivores-Water Column. The energy associated with consumers that utilize both plant and animal matter as energy sources. The dominant forms are: Mullet, crabs, Fundulus, and shrimp.

Table 3, continued

X_{20} - Carnivores-Water Column. The energy associated with consumers that utilize herbivores, omnivores, and other carnivores in the water column as energy sources. The dominant forms are: sharks, dolphin, rays, trout, flounder, Spot, Croaker, Drum and sea turtles.

X_{21} - Decomposers-Water Column. The total microbial biomass in the water column during ebb and flood tide as mgC/m^3 measured using ATP techniques. Basic measurement is ATP (luciferin/luciferase technique) and biomass carbon is calculated using a conversion factor of 250 mgC per 1 mg ATP /method of Holm-Hansen and Booth, 1966). The biomass of decomposers (mgC/m^3) is converted to energy ($kcal/m^3$) by literature values to obtain the energy associated with decomposers-water column. The dominant genera of bacteria are: Pseudomonas, Vibrio, Achromobacter, Aeromonas, and Cytophaga.

X_{22} - Dissolved Organic Matter (D.O.M)-Water Column. The energy associated with those dissolved organic chemicals in the water column synthesized by biological processes. These are mainly compounds arising from excretory and secretory processes.

System Parameters for Water Column Submodel

The system parameters, imports, and exports for the water column submodel are given in Table 4. Some of the values are literature values, others are best estimates from field experience. Several rate constants in the water column are unknown at this time, such as the rate constants associated with flow of energy from herbivores, omnivores, and carnivores to D.O.M. in the water column ($\lambda_{18,22}$; $\lambda_{19,22}$; $\lambda_{20,22}$). A "best guess" was used for these three rate constants. The feeding rates $\lambda_{18,19}$; $\lambda_{20,19}$; $\lambda_{18,20}$; $\lambda_{19,20}$ for the omnivores X_{19} and carnivores X_{20} were very hard to evaluate and estimates were placed on gut analysis studies.

System Matrix for Water Column Submodel

The system matrix $\underline{A}$ for the water column submodel is given in Figure 7. Normally, the diagonally dominant characteristic of the system matrix $\underline{A}$ insures system stability. However, in the water column submodel, the respiration energy loss of the biotic states was included in the export flows. Hence the system is not stable unless sufficient energy loss to account for respiration is considered in the export from each state. For the system matrix $\underline{A} = [A_{ij}]$, the sum of all columns is equal to zero, i.e.,

$$\sum_{i=1}^{7} A_{ij} = 0 \quad \forall j = 1, \ldots, 7.$$

For stability, the sum for each column should be negative.

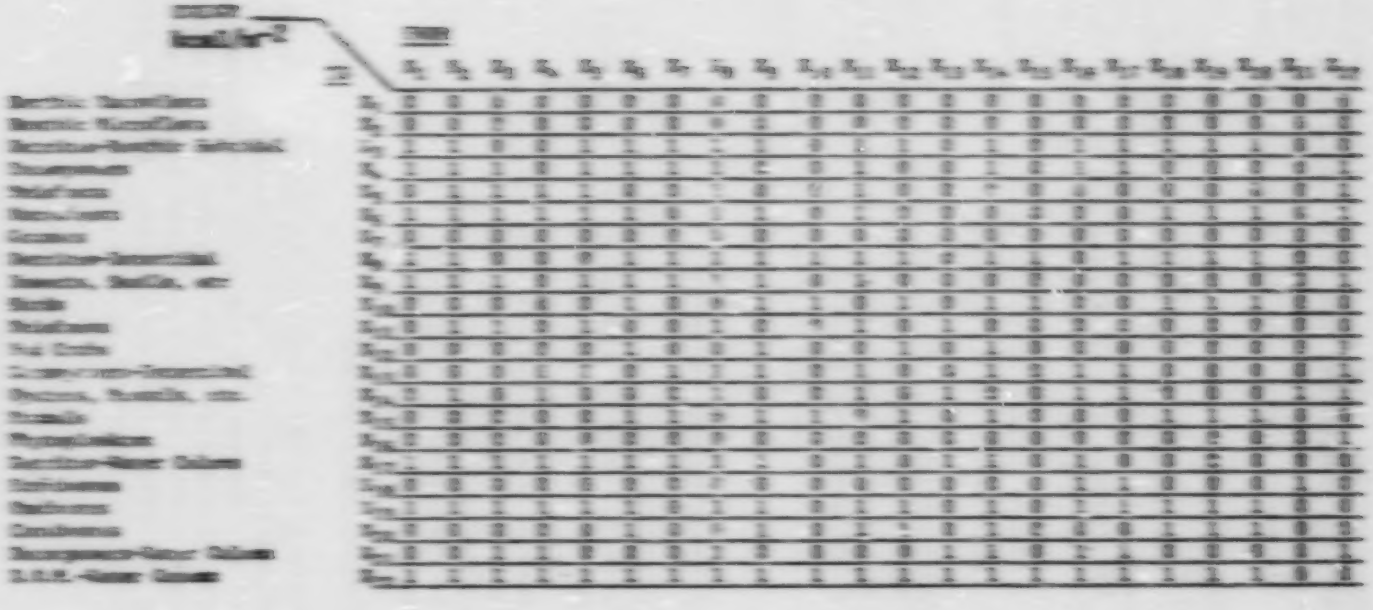

Figure 4. Selection matrix – North Inlet Survey.

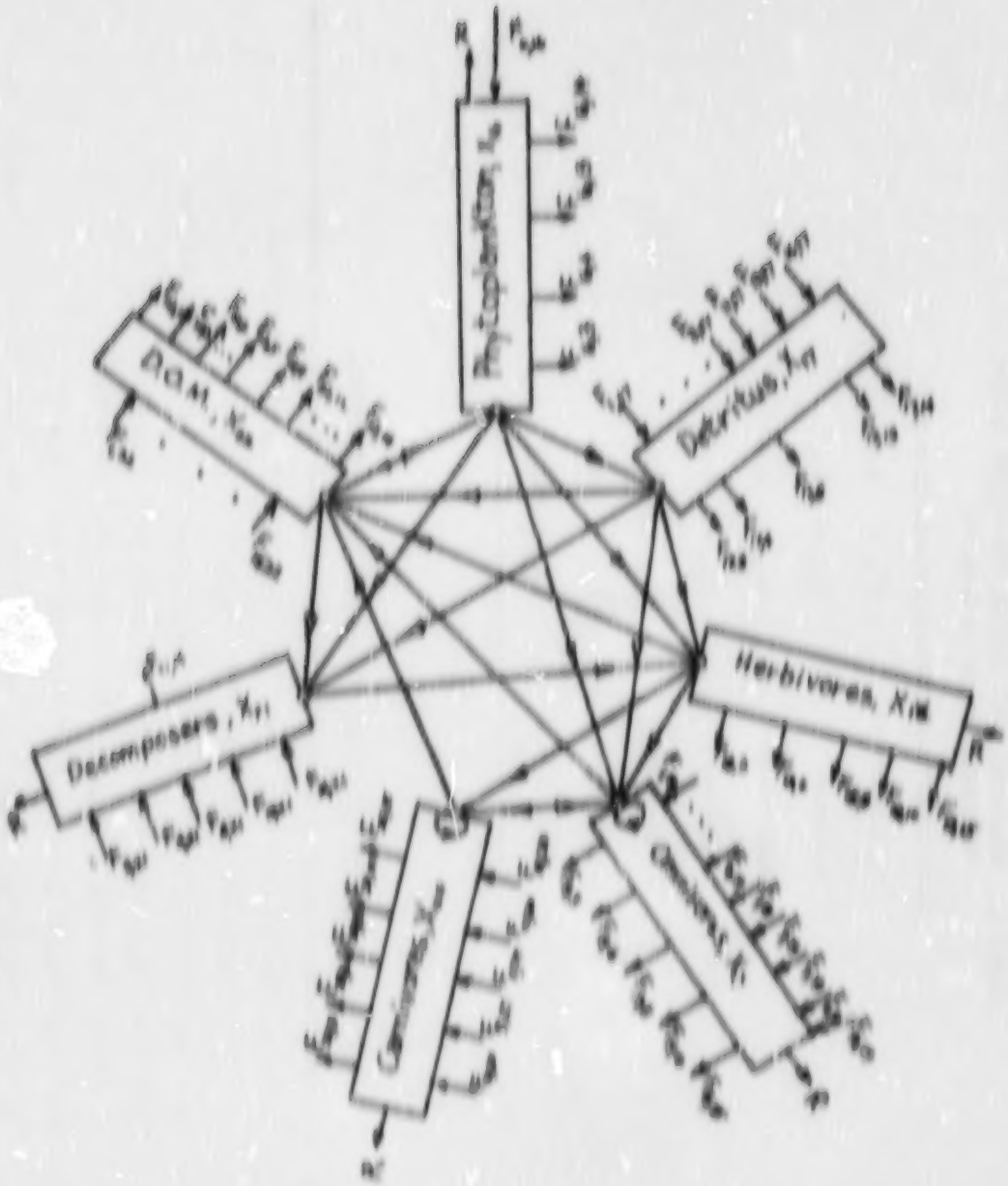

Figure 5. Water column submodel.

| | | |

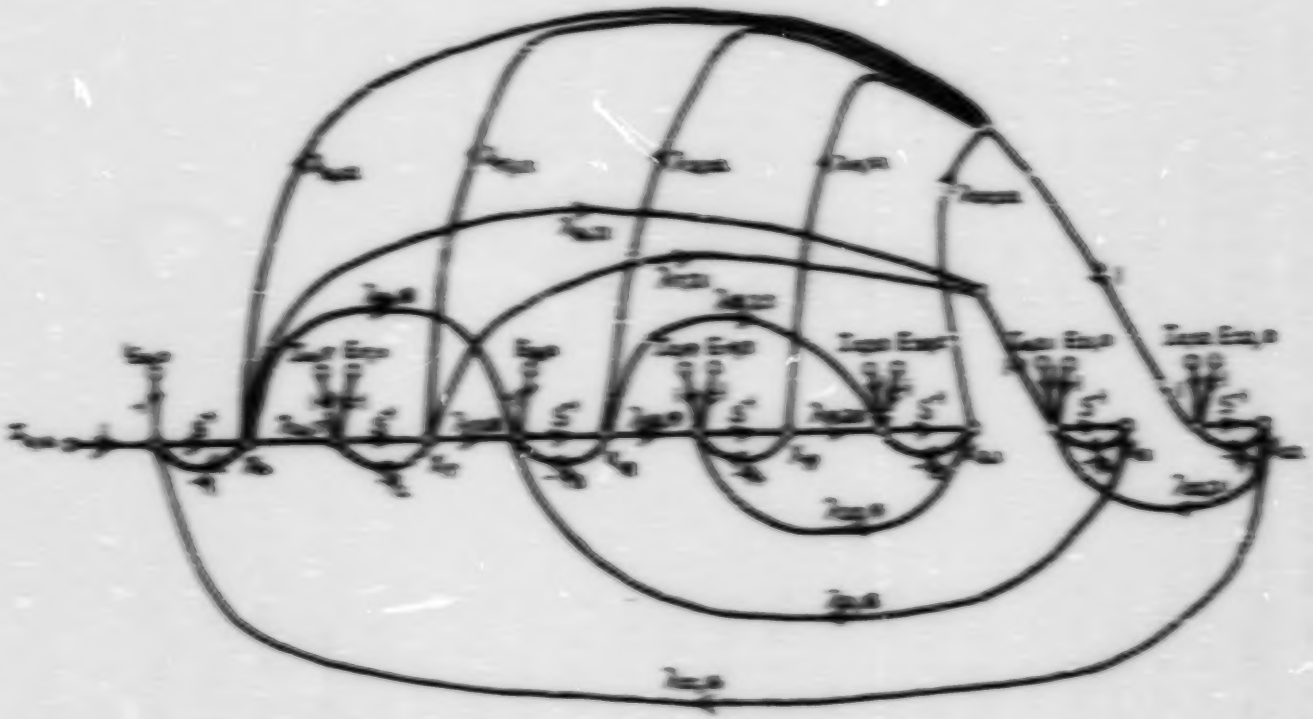

Figure 6. Signal flow graph for wave soliton network.

TABLE 4. SYSTEM PARAMETERS FOR WATER COLUMN SUBMODEL.

Flow Rates (day^{-1})	Imports, $I_{i,j}$ and Exports, $E_{i,j}$ ($kcalm^{-2}\ day^{-1}$)
$\lambda_{16,17} = 2.74 \times 10^{-5}$	$I_{0,16} = 9.01$
$\lambda_{16,18} = 2.19 \times 10^{-4}$	$I_{0,17} = 4.15 \times 10^{-2}$
$\lambda_{16,21} = 1.37 \times 10^{-4}$	$I_{0,19} = 1.32 \times 10^{-3}$
$\lambda_{16,22} = 2.19 \times 10^{-4}$	$I_{0,20} = 6.26 \times 10^{-4}$
$\lambda_{17,18} = 2.74 \times 10^{-4}$	$I_{0,21} = 1.84 \times 10^{-2}$
$\lambda_{17,21} = 5.48 \times 10^{-4}$	$I_{0,22} = 4.15 \times 10^{-1}$
$\lambda_{17,22} = 2.74 \times 10^{-5}$	$E_{16,0} = 9.00$
$\lambda_{18,19} = 6.38 \times 10^{-4}$	$E_{17,0} = 2.75 \times 10^{-2}$
$\lambda_{18,20} = 2.74 \times 10^{-4}$	$E_{18,0} = 3.52 \times 10^{-3}$
$\lambda_{18,22} = 2.74 \times 10^{-5}$	$E_{19,0} = 2.36 \times 10^{-3}$
$\lambda_{19,20} = 2.60 \times 10^{-4}$	$E_{20,0} = 2.50 \times 10^{-3}$
$\lambda_{19,22} = 1.37 \times 10^{-4}$	$E_{21,0} = 1.44 \times 10^{-1}$
$\lambda_{20,19} = 2.74 \times 10^{-4}$	$E_{22,0} = 3.01 \times 10^{-1}$
$\lambda_{20,22} = 1.37 \times 10^{-4}$	
$\lambda_{21,18} = 5.48 \times 10^{-5}$	
$\lambda_{21,22} = 0$	
$\lambda_{22,16} = 1.37 \times 10^{-5}$	
$\lambda_{22,21} = 6.85 \times 10^{-4}$	
$\phi_1 = \lambda_{16,17} + \lambda_{16,18} + \lambda_{16,21} + \lambda_{16,22}$	
$\phi_2 = \lambda_{17,18} + \lambda_{17,21} + \lambda_{17,22}$	
$\phi_3 = \lambda_{18,19} + \lambda_{18,20} + \lambda_{18,22}$	
$\phi_4 = \lambda_{19,20} + \lambda_{19,22}$	
$\phi_5 = \lambda_{20,19} + \lambda_{20,22}$	
$\phi_6 = \lambda_{21,18}$	
$\phi_7 = \lambda_{22,16} + \lambda_{22,21}$	

$$\underline{A} = \begin{bmatrix} -\phi_1 & 0 & 0 & 0 & 0 & 0 & \lambda_{22,16} \\ \lambda_{16,17} & -\phi_2 & 0 & 0 & 0 & 0 & 0 \\ \lambda_{16,18} & \lambda_{17,18} & -\phi_3 & 0 & 0 & \lambda_{21,18} & 0 \\ 0 & 0 & \lambda_{18,19} & -\phi_4 & \lambda_{20,19} & 0 & 0 \\ 0 & 0 & \lambda_{18,20} & \lambda_{19,20} & -\phi_5 & 0 & 0 \\ \lambda_{16,21} & \lambda_{17,21} & 0 & 0 & 0 & -\phi_6 & \lambda_{22,21} \\ \lambda_{16,22} & \lambda_{17,22} & \lambda_{18,22} & \lambda_{19,22} & \lambda_{20,22} & 0 & -\phi_7 \end{bmatrix}$$

Figure 7. The system matrix $\underline{A}$ for the water column submodel.

An obvious improvement in the model would be to model respiration and tidal washout separate from export. As noted by Mathelland and Kremer (1974), maintenance or stability of life can be viewed as a continual process of pumping out disorder in the form of heat loss through respiration to provide internal order within each compartment.

COMPUTER SIMULATION OF WATER COLUMN SUBMODEL

A CSMP-III program used to simulate the system of differential equations for the water column submodel was developed. A procedure for handling time-varying rate constants within a CSMP-III program was also developed. The development of software to simulate the water column submodel was not a problem since the CSMP-III language is designed for this type simulation.

CONCLUSIONS

A useful conceptual model for North Inlet Estuary has been developed. A "first attempt" dynamic model for the water column submodel has been formulated mathematically and a simulation program constructed. A great deal of work, however, is needed in the evaluation of system parameters.

A LINEAR SYSTEMS MODEL OF AN INTERTIDAL OYSTER COMMUNITY

Richard F. Dame and Stuart A. Stevens

ABSTRACT

Verbal, compartmental and mathematical models were developed for energy flow in the intertidal oyster community. Based on specific assumptions, simulation of the mathematical model indicated the original model was near stability. This agrees with field studies on the natural intertidal oyster communities in the North Inlet area which indicated that these oyster communities have been stable for the past five years. A LSA sensitivity analysis of the parameters in the mathematical model suggests the order in which these parameters should be studied. The linear systems model offers a first step in development of a resource management model for intertidal oysters.

INTRODUCTION

Intertidal oyster communities are common to high-salinity estuarine environments of the southeastern United States. These communities are dominated by dense concentrations of oysters, Crassostrea virginica, whose shells tend to give the assemblages a high degree of structural stability. The intertidal oyster communities or beds are located in the mid- to low-intertidal zone and usually border or project into tidal creeks. The oyster community has been compared to an industrialized city in that both are concentrations of consumers which depend on the flow of fuel and oxygen into the system and waste out of the system (Odum, 1971).

The intertidal oyster community is economically important as a source of commercial oysters and as a recreational zone for vacationers and coastal residents. Ecologically, intertidal oyster populations have been shown by Bahr (1974) and Dame (1976) to have high rates of energy flow. High energy flow is indicative of the oyster population's functional importance to estuarine systems. Because intertidal oyster communities are important, it is imperative that they be investigated as a system of interrelated populations interacting with their environment rather than as monoculture systems. Systems analysis is one approach to quantitative study of such systems.

Systems analysis is becoming more important as a research tool to ecology and resource management (Patten, 1971; 1972). It has been used extensively in the U. S. International Biological Program and currently is being used in the earliest stages of development in the North Inlet Ecosystem Project near Georgetown, South Carolina. The model and analysis described here is the first from the North Inlet Ecosystem Project.

The model presented here is only an initial step in which systems analysis is applied to the intertidal oyster communities of North Inlet. As more data become available and as our understanding of the North Inlet ecosystem and intertidal oyster communities improves, the model will become more sophisticated. The objectives of this first model of the intertidal oyster community are to summarize and indicate the limits of available data, point to new directions for research, and increase our understanding of oyster communities.

In this study, the intertidal oyster community is analyzed using energy and rates of energy flow as the main components of the model. Energy was chosen because it is universal in both biological and physical processes.

MODEL DEVELOPMENT

Every theory describing natural events is by necessity a simplification of the real world. Usually the first step in model building is a picture or verbal model of the system under consideration. In the case of the intertidal oyster community, a list of the organisms found in the community along with their biomass and numbers satisfies a verbal model (Table 5). Such a verbal model does not sort out the complexity of the intertidal oyster community; it describes what is there.

The next step in model development entails producing a model which describes to some extent the processes and structure of the intertidal oyster community. Since energy and energy flow were the processes and structural attributes we were most interested in understanding, we developed a compartmental model of energy flow (Fig. 8). The compartments describe the standing crops of herbivores (B_1), omnivores (B_2), carnivores (B_3), and decomposers (B_4) in kcal/m^2. The rates of energy flow into, out of and between the various compartments in the system are described by arrows.

Values for the standing crops and rate functions are given in Table 6. Some of these values are from observation on the North Inlet intertidal oyster communities while others are best estimates. The sources of the parameters in Table 6 are described below.

Standing crop values in gdw/m^2 (grams dry weight/m^2) for the herbivores, omnivores, and carnivores are from studies currently underway in North Inlet. These values are the means of seasonal observations during 1974. A value of 5 kcal/gdw was used to convert the dry weight biomass of

TABLE 5. INTERTIDAL OYSTER BED COMMUNITY BIOMASS AND NUMBERS.

Species	#/m²	g/m²	Trophic Level
Amphitrite ornata	3	0.430	Herbivore
Anurida maritima	14	0.611	Omnivore
Brachidontes exustus	741	93.350	Herbivore
Chione intapurpurea	1	0.157	Herbivore
Crassostrea virginica	974	164.870	Herbivore
Eurypanopeus depressus	61	5.700	Carnivore
Gammaridiana	6	0.008	Omnivore
Goubensia demissus	8	6.580	Herbivore
Glycera americana	1	0.016	Omnivore
Heteromastus filiformis	105	0.130	Omnivore
Insect pupae	3	0.013	Omnivore
Morphysa sanguinea	5	0.150	Omnivore
Nereis virida	7	0.021	Omnivore
Neresmaria neresmaria	4	4.380	Herbivore
Nereis succinea	109	0.717	Omnivore
Odontosyllis impressa	33	0.061	Carnivore
Panopeus herbstii	56	5.890	Carnivore
Phyllodoces fragilis	7	0.074	Omnivore
Uca pugilator	4	0.380	Omnivore

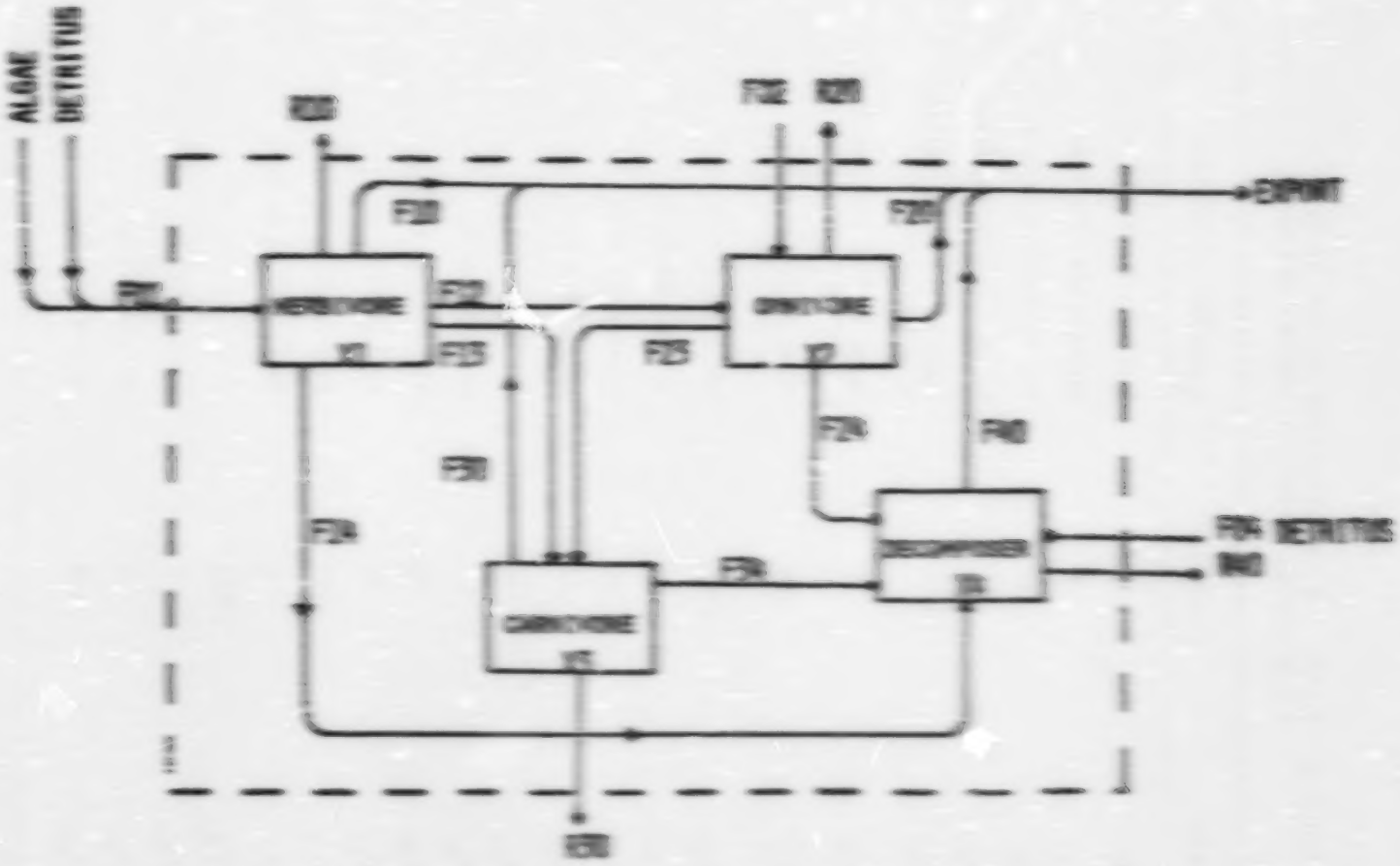

Figure 6. A compartment model of energy flow in an intertidal oyster community.

TABLE 6. VALUES FOR THE FUNCTIONS IN THE INTERTIDAL OYSTER COMMUNITY COMPARTMENT MODEL.

Function	Kcal/m^2/yr	Definition of Function
S_1	2449	Herbivore Standing Crop
S_2	8	Omnivore Standing Crop
S_3	58	Carnivore Standing Crop
S_4	1	Decomposer Standing Crop
F_{01}	17011	Input of Algae and Detritus to Compartment S_1
F_{02}	15	Input of Algae and Detritus to Compartment S_2
F_{04}	100	Input of Detritus to to Compartment S_4
R_{10}	9980	Respiration by S_1
R_{20}	19	Respiration by S_2
R_{30}	56	Respiration by S_3
R_{40}	808	Respiration by S_4
F_{14}	749	Mortality of S_1
F_{24}	37	Mortality of S_2
F_{34}	59	Mortality of S_3
F_{12}	44	Feeding by S_2 on S_1
F_{13}	133	Feeding by S_3 on S_1
F_{23}	6	Feeding by S_3 on S_2
F_{10}	10113	Export from S_1
F_{20}	7	Export from S_2
F_{30}	56	Export from S_3
F_{40}	100	Export from S_4

invertebrates into standing crop energy (Cummings, 1961) and the methodology of Dame (1972; 1976) was used to account for the energy retained in bivalve shells. No measurements were made of decomposer biomass, so an estimate of 1.0 kcal/m^2 was chosen. This estimate is close to a value of 0.14 g/m^2 of decomposers observed by Harvey (1950).

Five years of observations of the intertidal oyster beds in North Inlet indicate there is little change in biomass and diversity (Dame, 1976; unpublished data). It was assumed from these observations that the intertidal oyster community model is at steady state, where inputs to X_1 (P_{01}) from algae and detritus was calculated by summing the total outputs from X_1 and setting this value equal to P_{01}. Input of detritus to X_2 (P_{02}) was considered as 25% of the total input required to equal the outputs from decomposers, therefore input of detritus to X_4 (P_{04}) was considered equal to export X_4 (P_{40}) to achieve a balanced model.

Respiration values were taken from the literature or calculated from equations using dry body weights. Respiration estimates for oysters and other bivalve herbivores (R_{10}) were based on observations of Dame (1972 and unpublished). Respiration of carnivorous crabs (R_{30}) was estimated from observations of Dame and Vernberg (in prep) while values for the other macrofauna were computed using the general equation of Paraketsat (1968). Decomposer respiration (R_{40}) was set equal to the sum of the input of mortality to this compartment.

Mortality was calculated from turnover time for a given compartment. Turnover times used were: herbivores - 3.3 years (Dame, 1976), omnivores - 0.3 years (D. M. Dauer, personal communication), and carnivores - 1.5 years (Dame and Vernberg, in prep).

Feeding by omnivores on herbivores (F_{12}) was calculated by taking 75% of the total inputs needed to balance the sum of the outputs from X_2. Feeding by carnivores on herbivores (F_{13}) was found by summing the outputs from X_3, taking a feeding input of 50% of the total omnivore production (F_{23}), and allowing the remainder of the required input to come from herbivores.

Export from the system was in the form of feces, pseudofeces, and feeding by transient carnivores. Production was estimated for the various components from Dame (1976), Dame and Vernberg (in prep) and the general equations developed by McNeil and Lawton (1970). Utilizing an assimilation efficiency for oysters of 0.62 (Dame, 1972) export of feces and pseudofeces was computed. The export of feces and pseudofeces from X_2 and X_3 was estimated to be 14% of the standing crop biomass of the respective compartments. X_4 export was set equal to X_4 input of detritus as previously stated. Predation of X_1 by carnivores external to the system was found by subtracting the remainder of production. Export from X_2 to transient carnivores was equated as 50% of the total omnivore production. A value of 100% of the carnivore production was used as feeding by

external carnivores on E_3, since there are no predators on this compartment within the system's boundaries.

The next stage in modeling the system was to develop a mathematical model which described amounts and rates of energy flow by a set of ordinary differential equations. Transfer coefficients were computed for the steady state by dividing the rate of energy leaving a compartment by the amount of energy contained in the compartment. Transfer coefficients for the intertidal oyster community model are shown below, the Greek letters ρ, λ, μ, and τ stand for respiration, export from the system, export to decomposers when organisms died, and predation within the system.

$\rho_{10} = 3.4$	$\lambda_{10} = 4.13$	$\mu_{14} = 0.30$	$\tau_{12} = 0.02$
$\rho_{20} = 2.36$	$\lambda_{20} = 0.86$	$\mu_{24} = 3.33$	$\tau_{13} = 0.05$
$\rho_{30} = 0.95$	$\lambda_{30} = 0.50$	$\mu_{34} = 0.67$	$\tau_{23} = 0.72$
$\rho_{40} = 734.70$	$\lambda_{40} = 90.91$		

By assuming that energy transferred from a donor compartment to a receiving compartment is directly proportional to energy in the donor compartment, and by expressing all energy losses and gains from a compartment in terms of transfer coefficients, the system can be defined by the following set of differential equations, one equation for each compartment.

$$dN_1/dt = F_{01} - N_1 (\rho_{10} + \lambda_{10} + \mu_{14} + \tau_{12} + \tau_{13}) \quad (1)$$

$$dN_2/dt = F_{02} + \tau_{12}(N_1) - N_2 (\rho_{20} + \lambda_{20} + \mu_{24} + \tau_{23}) \quad (2)$$

$$dN_3/dt = \tau_{13}(N_1) + \tau_{23}(N_2) - N_3(\rho_{30} + \lambda_{30} + \mu_{34}) \quad (3)$$

$$dN_4/dt = F_{04} + \mu_{14}(N_1) + \mu_{24}(N_2) + \mu_{34}(N_3) - N_4 (\rho_{40} + \lambda_{40}) \quad (4)$$

As previously defined, N_n describes the standing crop energy of a given compartment and F_{01}, F_{02}, and F_{04} are forcing functions for energy entering an intertidal oyster community system.

The differential equations were solved simultaneously utilizing Continuous Systems Modeling Program III (CSMP III) as described by Patten (1971) on an IBM 370/165 digital computer. All compartments of the system reached steady state within 2.2 years. The herbivores (N_1) reached a steady state value of 2469.3 kcal/m^2 at 0.725 years. The omnivores (N_2) became stable at 0.650 years with a standing crop of 8.0957 kcal/m^2. The carnivores followed with a time of 2.025 years and a biomass of 58.194 kcal/m^2. The decomposers required the most time to stabilize, 2.2 years with a value of 1.0097 kcal/m^2 with caloric charges low and with steady state quickly reached.

The model was analyzed for statistical sensitivity at steady state. In this case, sensitivity analysis indicates how the individual compartments behave if a given rate function is changed 1%. The results of the sensitivity analysis are shown in Table 7.

The 1% sensitivity analysis of the intertidal oyster community model shows that the standing crops of all compartments are most sensitive to changes in energy input (F_{01}) to the X_1 compartment. This is expected in a simple linear model. In addition, all four compartments exhibited a high level of sensitivity to changes in export (λ_{10}) and respiration (ρ_{10}) from X_1. All compartments were fairly sensitive to change in their respective respiration energy losses. Compartment X_3, the omnivores, was also sensitive to energy losses to the decomposers (μ_{34}) and external to the system (λ_{30}). Finally, the decomposers (X_4) were very sensitive to changes in respiration, energy loss (ρ_{40}) and energy input from the herbivores (μ_{14}). Using this sensitivity analysis of the intertidal oyster community model as a guide, it is easy to develop a hierarchy of transfer functions for future study.

DISCUSSION

The linear systems model of the intertidal oyster community reached stability in a short period of time (2.2 years) and this seems to describe the naturally occurring intertidal oyster communities in North Inlet which have been stable for at least the past five years. We cannot at this time say that this model is a valid representation of the "real world" intertidal oyster communities until we have manipulated and stressed existing intertidal oyster beds and simulations of the model have predicted the changes which our manipulations produce in the real communities.

The linear character of the intertidal oyster community systems model may have to be changed, especially in respect to the feeding rates of the herbivores, beyond their needs, the herbivores will not in nature continue to grow (Tenore and Dunstan, 1973; Winter, 1973). One possibility might be to model the herbivore feeding rates with some feedback repression in a manner similar to the procedure described by Wiegert (1975). It can be argued, particularly by biologists, that a predominantly linear model of an ecosystem or community is unrealistic, but it should be noted that linearization may describe ecological systems in their large scale better than non-linear models (Patten, 1975).

The development of a linear systems model of the intertidal oyster community has noted shortcomings in that there is a paucity of available data. There are no quantitative data on the export of energy from the community by transient predators, although we know that these predators exist. The feeding rates of most of the organisms in the model are only vaguely known, if at all. We also need to know the magnitude of detritus and algal food sources available to the filter feeding herbivores since their feeding rates are very sensitive to change, the decomposer component

standing crop and the sensitivity of decomposer respiration, and the importance of the meiofauna of the intertidal zone to intertidal oyster communities.

The present systems model of the intertidal oyster community forms a basis for the development of a new type of shellfish management model which relates all segments of the system to the management process. The model presented here is only a first step and future models will include additional observations on many of the energy fluxes not observed to date, seasonal changes in standing crops and the influences of the environment, particularly temperature and salinity, on the rates of flow into, out of, and within the system.

TABLE 7. IS SENSITIVITY OF THE LINEAR SYSTEMS MODEL OF THE OYSTER COMMUNITY.

Rate Functions and Coefficients	% Change in Standing Crops			
	X_1	X_2	X_3	X_4
F01	1.000	0.753	0.977	0.883
F02		0.224	0.011	0.083
F04				0.110
ρ10	0.155	0.064	0.046	0.010
λ10	0.595	0.446	0.581	0.934
μ14	0.044	0.033	0.043	0.779
γ12	0.003	0.747	0.031	0.023
γ13	0.007	0.005	0.007	0.006
ρ20		0.225	0.015	0.011
λ20		0 119	0.005	0.004
μ24		0.046	0.002	0.003
γ23		0.099	0.041	0.001
ρ30			0.430	0.018
λ30			0.283	0.011
μ34			0.301	0.038
ρ40				0.879
λ40				0.116

STUDIES ON THE PHYTOPLANKTON AND MICROBENTHIC ALGAE IN THE NORTH INLET ESTUARY, S. C.

Richard G. Zingmark

It is well known that, because of their generally high productivity, estuaries play a major role in supporting numerous fish and invertebrate species during at least some phase of their life histories (Lauff, 1967; McHugh, 1967). It has been estimated that two-thirds to three-fourths of the carbon fixed in East Coast salt marsh estuaries originates from the autotrophic production of halophytic spermatophytes such as Spartina alterniflora, and is utilized by consumers in the form of detritus (Teal, 1962). The remaining carbon is contributed largely by algae on the marsh mud, phytoplankton in the water column, the "suwuchs" community on halophytes, and, to a lesser extent, by the macrobenthic algae (Pomeroy, 1959; Ragotzkie, 1959; Sasaki and Odum, 1961; Marshall et al., 1971). The plankton communities associated with the surface film perhaps are also significant sources of energy to salt marsh estuaries (Gallagher, 1975).

Studies on productivity of phytoplankton in the North Inlet estuary, S. C. were begun in 1972 because it is a significant trophic component of this ecosystem. It is essential that an ecosystem model consider all of the sources and sinks of energy within and without the system. Thus, it was required that we quantify the energetics of the primary producers in North Inlet. The major objective of this study was to determine the annual production of energy by the smaller algae in North Inlet. Annual variations in biomass and productivity of phytoplankton and benthic microflora were measured.

DISCUSSION

The rate of phytoplanktonic production of 273 g C/m/year, measured during this study (1974-75), was about one third lower than the rate measured in North Inlet in 1972-73 (Sellner et al., 1976). As the techniques used in both studies were identical, the differences in the two studies are assumed to reflect annual variations in productivity. Both rates are lower than a few other studies (Riley, 1956; Strosa and Stottlemeyer, 1965; Thomas, 1966), but are significantly higher than those measured in nearby estuaries to the south (Ragotzkie, 1959) and to the north (Williams, 1966; Williams and Murdoch, 1966; Thayer, 1971). The reasons why the present data are about 4-5 times larger than those of

estuarine waters of North Carolina are unclear. The annual ranges of environmental factors such as temperature, salinity, and pH in North Inlet were not significantly different from those in North Carolina. This would allow photosynthesis to occur throughout a deeper water column. Thayer (1971) showed that the productivity rate on a m^3 basis was about the same as an areal (m^2) basis. Thus, the depth of the photic zone in Beaufort, N. C. estuaries must be about 1 M. In North Inlet the depth that receives one percent of the surface isolation was calculated to be 3.3 m. All other environmental factors being equal, the increased depth available for photosynthesis in North Inlet could account for the significant difference in productivity measured elsewhere. Thus, light may be the most controlling, limiting factor in southeastern coastal estuaries. However, without comparative data on nutrient concentrations from the two areas, the differences can never be fully resolved.

PRODUCTION OF THE BENTHIC MICROFLORA

There were significant differences in the benthic productivity rates in the shallow creek station from those of the other stations. The differences cannot be explained on the basis of light, as the average Secchi disc readings at the shallow station were not significantly different from those at other stations. The biomass, as measured by functional chlorophyll, was significantly lower than at other stations. In January, the bloom of Vaucheria sp. that occurred at the shallow station was reflected by significantly higher productivity than at other stations. Such blooms of Vaucheria have been reported from elsewhere (Taylor, 1969; Simons, 1974).

Of some concern was the magnitude of the productivity of the benthic microflora as compared to other studies. An annual rate of 693 $g/m^2/yr$ (i.e. 1.90 $g/m^2/day$) is over three times greater than any annual rate for benthic algal productivity found in the literature (Table 8). There are at least three possible explanations: 1) my values are correct and the North Inlet is a unique, highly productive estuary; 2) my values are incorrect because of some gross technical or computational error; or 3) my values are the correct order of magnitude, while the values in the literature are underestimated. I can reasonably discuss explanations 1) and 2) but, not 3). As I have checked and rechecked my computations and have tested and calibrated the sampling, incubation, processing, and enumerative techniques, I am confident that my values are correct. Further, reports in the literature indicate that benthic productivity may be up to about twice that of the phytoplankton (Marshall et al., 1971). The rate of benthic productivity in this study was 2.3 times that of the phytoplankton productivity. I am left with the possibility that North Inlet is a unique estuary.

RELATIONSHIP BETWEEN PRODUCTION AND TEMPERATURE

Salinity, temperature, pH, and transparency in the North Inlet estuary seemed to be suitable for growth of algae throughout the year. There was a pronounced seasonal cycle in production of phytoplankton

TABLE 8. ANNUAL RATES OF BENTHIC ALGAL PRODUCTIVITY AS REPORTED IN THE LITERATURE.

Location	Method of Measurement	Rate of Production g C · M^{-2} · yr^{-1}	Reference
Georgia estuary	O_2	200	Pomeroy(1959)
Puget Sound	O_2	143-226	Pamatmat(1968)
Danish lake	^{14}C	143	Hunding(1971)
Western Wadden Sea	^{14}C	100 ± 40	Cadée and Hegeman(1974)
Danish Wadden Sea	^{14}C	115-178	Grønved (1962)
Danish fjords	^{14}C	116	Grønved (1960)
New England estuaries	^{14}C	61	Marshall et al.(1971)
Scottish estuary	^{14}C	31	Leach (1970)
Intertidal sandy beach	^{14}C	4-9	Steele and Baird (1968)

and benthic microalgae, however, that was highly correlated with the seasonal variation in water temperature. Such correlations with temperature are characteristic of shallow, high salinity estuaries of widely separated areas such as Massachusetts, Long Island, North Carolina, Italy, and Denmark. Many of these studies attribute the correlation to a dependency of the rate of nutrient regeneration on temperature (Riley, 1941; 1956; Steemann-Nielsen, 1958; Grønved, 1960; Vatova, 1961; Ryther, 1963; Williams, 1966; 1973; Williams and Murdoch, 1966; Thayer, 1971; Seliner et al., 1976). Whether nutrient regeneration was regulated in part or wholly by the temperature of North Inlet is not known, as nutrients were not measured during this study. However, Thayer (1971) reported evidence that seasonal changes in nitrate and phosphate concentrations in Beaufort, N. C. were influenced by temperature, microbial immobilization and remineralization, and phytoplanktonic utilization. The fact that changes in temperature cause changes in rates of metabolic processes may also explain the data.

STANDING CROP OF THE PHYTOPLANKTON AND BENTHIC MICROALGAE

Concentrations of phytoplankton in North Inlet were reported to vary annually between 1.04 and 3.40 x 10^6 cells/l (Seliner et al., 1976) with no indication of a seasonal cycle. In contrast, there was a pronounced

seasonal cycle in functional chlorophyll a concentrations of both phytoplankton and benthic microalgae in the present study, which coincided with annual temperature cycles. The similarity in concentrations of functional phytoplanktonic pigments at all stations and at all depths indicates that the standing crop of phytoplankton was unstratified and mixed. The average concentration of chlorophyll a in North Inlet was 9.61 mg Chl a/m^3 while that at Beaufort, N. C. was approximately 3.8-4.3 mg Chl a/m^3 (Williams and Murdoch, 1966; Thayer, 1971). These are actually comparable values on a m^3 basis, when one realizes that the average depth of the photic zone in North Inlet is about three times that of the Beaufort, N. C. estuaries (Thayer, 1971). The annual mean Fo/Fa ratio (fluorescence before and after addition of acid, a measure of living chlorophyll) of the phytoplanktonic chlorophyll of 1.70 indicates that the phytoplankton of North Inlet were reasonably productive (Yentsch, 1965).

Microbial biomass (including bacteria, algae, protozoa and fungi) in estuarine sediments can be greater than that of the water column by several orders of magnitude (Zobell, 1946; Ferguson and Murdoch, 1975). The standing crop of benthic microalgae in the present study was greater than that of phytoplankton by 193 to 374 times. The standing crop at the shallow station averaged almost two times less functional chlorophyll than at the others. Presence of a bloom of Vaucheria sp. in January was evident in elevated concentrations of chlorophyll at the shallow station and the biomass of the benthic meiofauna showed a marked increase following the bloom of Vaucheria (B. C. Coull, personal communication). The appearance of this bloom was not correlated with a rise in temperature. It is not possible to compare my benthic chlorophyll data with most other papers, as other investigators reported chlorophyll as mg Chl/g/dry wt (Leach, 1970; Cadée and Hegeman, 1974). However, the annual concentration of chlorophyll in North Inlet was similar to that reported by Ferguson and Murdoch (1975) for Beaufort, N. C. and about 10 times as great as data reported by Marshall et al. (1971) for southern New England. The annual mean Fo/Fa ratio of 1.36 at Station 1 was quite low, indicating that a significant amount of non-functional chlorophyll as well as phaeophytins, phaeophorbides and other degradation products of chlorophyll were present in the sediments. Such pigment products are commonly found in aquatic sediments (Daley et al., 1971). The mean Fo/Fa ratio of 1.60 at the deeper stations indicated a healthier and potentially more productive benthic microalgal community than at the shallow station. This was confirmed by the productivity data.

CONCLUSIONS

The above-ground production of halophytes in North Inlet, mainly Spartina alterniflora, has been estimated as about 900 g/m^2/yr (J. H. Dean, personal communication). Considering the productivity data reported here, phytoplankton, together with benthic microflora, fix an amount of carbon per year equivalent to the halophytes. Since the "auf wuchs" community, the benthic macroalgae and the surface film community (Gallagher, 1975) is not considered, it appears from the above data that in North Inlet, the

algae are the most important primary producers. If this is true, then our concepts regarding the relative ecological significances of the various plant communities in salt marsh estuaries must be revised. At the very least the algae must be considered as an important trophic compartment in our model of the North Inlet Ecosystem.

COMPOSITION AND SEASONALITY OF THE NORTH INLET ZOOPLANKTON: ESTABLISHMENT OF THE BASELINE

Bruce T. Coull

ABSTRACT

Zooplankton of the North Inlet estuary near Georgetown, South Carolina were collected bi-weekly from January 1974 to August 1975 at four stations. Zooplankton numbers ranged from 177 to 84,414/m^3 ($\bar{x}$ = 9236/m^3) and biomass from 540 to 140,169 µg dry weight/m^3). The major peak in density of zooplankton occurred between April-July both years.

Copepods (including larval stages) were the most dominant taxon, comprising 64-69% of total zooplankton numbers and biomass. The most common species were Paracalanus crassirostris, Acartia tonsa, Oithona colcarva, and Eutorpina acutifrons. Cirripedia naupli were the most common meroplankter comprising 13% of the total for the entire sampling period. Other important groups were bivalve and polychaete larvae and Oikopleura sp. Comparison of the major species of copepods and their reproductive periodicities with those reported in the literature suggests that the North Inlet fauna is most closely allied to that of Florida waters.

INTRODUCTION

To date, composition of the South Carolina zooplankton is virtually unknown. Along the Atlantic coast, studies have extended south to North Carolina (Thayer et al., 1974) and from Florida to the Caribbean (Grice, 1960; Gonzalez and Bowman, 1965). South Carolina may represent a transition zone between the north-temperate, mid-Atlantic coast and the tropical waters of Florida and the Caribbean, and as part of an intensive ecosystems analysis of the North Inlet estuary, it was imperative to obtain basic information on the zooplankton in order to provide the information requisite for a trophic model of the estuary.

Since the first phase of any community study must provide baseline analyses of the component fauna as a reference for future studies, this study dealt with specifying the zooplanktonic taxa (particularly the copepods), their densities, and their standing crops. Further, the North Inlet zooplankton was compared to those reported from other areas of the

Atlantic coast using a similarity matrix to determine to what area the North Inlet fauna was most closely allied.

DISCUSSION

Unlike many temperate regions where zooplankton exhibit spring and fall blooms together with a summer ebb, the North Inlet zooplankton attained maximum abundance in the summer. Greatest numbers were found from June through mid-July; a pattern also reported for the phytoplankton in North Inlet by Seliner (1973), who found that primary production increased with temperature and was maximal in summer. Thus, the observed summer maximum of zooplankton was concurrent with that of the phytoplankton.

Numbers and biomass indicate that Stations B and C, located in ebb channels, had the highest "productivity" averaged over the year. Station A was located off of a major creek in which Winyah Bay waters may flow into North Inlet. The creek is 1-1.5 m deep and 4 m wide at low tide. Station B was located in the main ebb channel of the North Inlet (700-800 m wide at low tide) in 4-5 m of water. This locale is representative of a fairly predictable environment in terms of temperature and salinity, having a direct connection with the offshore, oceanic waters. Additionally, in this area, offshore waters enter into the estuary on flood tide. Station C was located in an ebb-oriented channel (200-500 m wide at low tide) off the main arm of the oceanic channel in 1-1.5 m of water. Station D was located at the upper reaches of a Spartina marsh.

The zooplankton at B and C were approximately two times more abundant than at Stations A or D; differences that are statistically significant ($\alpha = 0.05$). Highest zooplankton densities were found at Station B in most of the months and only on very few occasions did the densities at C exceed those at B. In comparing the two upper tidal reach stations (A and D) Station A, proximal to Winyah Bay, was consistently less populated than Station D which was located well within the North Inlet system. Since there was a net flow of water out of the inlet when averaged over time (Kjerfve et al., 1975), the higher densities at Station B and/or C might be attributed to recruitment of planktors from the upper reaches of the marsh. Since there is a funneling effect, large amounts of the zooplankton would be washed out of the marsh and into the inlet and perhaps into the outer coastal waters. As stated before, Stations B and C were located in ebb channels, B being located in the major one for the entire estuary. Hence, Station B had recruitment from a larger area of the marsh than Station C. This accounts, in part, for higher numbers and biomass there.

The average number of zooplankton in the North Inlet (9214/m^3) is comparable to figures reported for estuaries along the Atlantic coast, 8501/m^3 and 4000-8000/m^3 (Gage and Herman, 1972 and Thayer et al., 1974, respectively). The mean dry weight in North Inlet, 16,009 ug/m^3, is also within the range of a North Carolina estuary, 14,000-21,000 ug/m^3 (Thayer et al., 1974).

Total number of organisms is often used as the main indicator of the fraction of the total biomass contributed by one species. This index alone can be misleading when considering the trophic importance of the various components of the zooplankton (Reeve, 1970). For example, in our study, the copepod Paracalanus crassirostris was significantly more dominant in terms of numbers than Acartia tonsa, but there was no statistical ($\alpha = 0.05$) difference between the two species in total biomass. Although numbers of A. tonsa and Oithona colcarva were not statistically different, A. tonsa dominated in terms of biomass. Therefore, both numbers and biomass are important components to consider in a discussion of zooplankton population dynamics. Paracalanus crassirostris is one of the smallest calanoid copepods (Davis, 1944) and we found it weighed three times less than A. tonsa. Since smaller animals characteristically have higher metabolic rates per unit of body weight when compared to larger ones (Zeuthen, 1953), P. crassirostris was probably the most energetically important species in the plankton.

Hutchinson (1967) believed that a body size factor difference of 1.33 is sufficient to allow separation of food resources in co-occurring copepod species. Therefore, although P. crassirostris and A. tonsa occur concurrently, their difference in size may reduce competition for food resources. On the other hand, O. colcarva and P. crassirostris were similar in size, thus other mechanisms must be important in fractionating the food resources of these species (Haly and Haly, 1974). This abundance-size relationship may reflect, to some extent, resource partioning in these species of copepods.

The abundance of small copepods may also impart some competitive advantage with respect to predation pressures for species which occur year-round in the plankton. Larval fishes prey on zooplankton; Acartia, Centropages, Temora and Eurytemora are common prey for pinfish, spot and menhaden (Thayer et al., 1974). Preliminary observations on the larval fishes in North Inlet indicate a year-round production of these and/or associated species (J. M. Dean, personal communication). Vertebrate predation pressure is selectively greater on larger zooplankton (Heavey, 1964; Brooks and Dodson, 1965) and since the North Inlet zooplankton is dominated by small species and fishes, grazing presumably takes place year-round and the small species may be at a competitive advantage in such a system.

Dominance of copepods in plankton is a common phenomenon. Herman et al. (1968) found that copepods comprised 98.1% of the total zooplankton in a Maryland estuary, Sage and Herman (1972) reported 84% in New Jersey, and Thayer et al. (1974) found it to be 81% by numbers and 84% by dry weight in North Carolina. In North Inlet, the copepods comprised only 68-67% of the total zooplankton numbers and biomass, primarily because meroplanktonic forms comprised a larger segment of the population here than elsewhere. Cirripedia nauplii made up 13% of the North Inlet zooplankton and Herman et al. (1968) reported a figure of less than 1%. Similarly, in North Inlet, bivalve, gastropod and polychaete larvae comprised 12% of the fauna while in the Herman et al. study this figure was less than 1%.

North Inlet zooplankton did not exhibit the successional pattern typical of mid-Atlantic and northern estuaries where Acartia clausii (a winter-spring form) replaced A. tonsa (a summer-fall form) and vice-versa (Jeffries, 1962). Acartia clausii did not occur in the North Inlet plankton but this was not unexpected since Sutcliffe (1949) noted its absence from Beaufort, North Carolina plankton. Woodmansee (1958) described the replacement of A. tonsa in the winter and spring by Paracalanus parvus in the tropical waters of Florida. However, in North Inlet P. crassirostris and A. tonsa did not exhibit this type of successional or replacement pattern; both species were abundant throughout the year. Thus, even if P. crassirostris is considered the "niche equivalent" of P. parvus, there is no apparent correlation with the results of Woodmansee (1958). Although P. parvus is reported both north and south of North Inlet (Sutcliffe, 1949; Reeve, 1970), there was no evidence of this species being present. However, due to the large numbers of Paracalanus encountered, not every individual was examined under a compound microscope. If P. parvus did, in fact, occur in North Inlet, it must have been of minor importance.

Copepod species composition and seasonal distribution in the North Inlet estuary were very similar to those reported by Orice (1960) from Florida. He reported a year-round production of the six most common species, including Acartia tonsa and Oithona colcarva, although there were fluctuations in their densities. As in North Inlet, P. crassirostris was the most abundant species along the inshore Florida coast and showed a year-round reproductive pattern. Orice (1960) also found that O. venusta was a year-round reproducer with no particular pattern in reproduction and that Centropages hamatus bred in the winter. Sutcliffe (1949) found this to be true of C. hamatus in North Carolina while Centropages typicus was observed only in very low numbers in June. Another year-round producing copepod in North Inlet, Eutarpina acutifrons, is very cosmopolitan and has been reported to have a world-wide distribution in tropical and subtropical waters (Gonsales and Bowman, 1965). Moreover, Weiss and Hopkins (1975) reported Oithona brevicornis (colcarva), A. tonsa, and P. crassirostris as the dominant zooplankton species in a Florida estuary.

Other data which are in agreement with that of Orice (1960) were the presence of Saphirella sp., and that Labidocera aestiva breeds in late spring and summer. However, in North Inlet, this pattern was extended to the early portion of the winter. Fleminger (1956) stated that L. aestiva was representative of a northern temperate coastal area while Labidocera scottii was representative of a tropical or near-tropical coastal area. Labidocera scottii was not found in our study. Thus, the North Inlet zooplankton is more closely allied than that from more northern regions to that of the Florida region, since many of the species are tropical forms and most exhibit reproductive patterns characteristic of this area.

In order to approach the study of community structure of the North Inlet, we compared our data with other areas of the eastern Atlantic coast. The comparison of diversity indices, H' and J, of the North Inlet with these other zooplankton studies suggests that the different estuarine

regimes are indistinguishable. Furthermore, it is noteworthy that the indices obtained from the Patuxent River Estuary, Sandy Hook Bay area and North Inlet are quite similar to that of an inshore station in Bermuda despite the fact that the species compositions of these four stations are very dissimilar.

Additionally, throughout the year, the diversity indices calculated on North Inlet zooplankton remained virtually unchanged (1 one standard deviation) while composition of the species of copepods changed to some extent with the seasons (one exception to the diversity consistency). Thus, within North Inlet and other areas, there appears to be a rather constant "diversity" for estuarine, inshore coastal zooplankton assemblages. The zooplankton community of North Inlet is very much like other systems of the East Coast in terms of diversity, and these diversity values may represent a standard range which any estuarine zooplankton community may be expected to attain.

VERTICAL MIGRATION OF LARVAL *UCA* IN NORTH INLET ESTUARY

F. DeCoursey

ABSTRACT

Stage I *Uca* zoeae in a main ebb channel of the North Inlet Estuary undergo regular changes in numbers and vertical position. Maximum numbers are found at the time of low and rising tides. Concentration in the lower quarter of the water column occurs at this time.

INTRODUCTION

Vertical migration in the ocean water column has been shown to be a feature of many mid-water planktors (Cushing 1951, 1955; Bainbridge, 1961; Diets, 1962; Woodmansee, 1966; Pearre, 1973; Budjakov and Vorobina, 1975). Since the discovery in the early 1940's that the DSL (deep scattering layer) of open ocean waters correlates closely with movements of small nocturnal animals (Diets, 1962), the study of vertical migration has made rapid strides (Boden, 1962; Barham, 1961; 1966; Kampa, 1971; Beamish, 1971; Donaldson and Pearcy, 1972; Isaac et al., 1974). Consisting primarily of myctophid fishes and euphausiid shrimp, the layers range from 300-600 m in depth during the day, then move toward the surface at night (Diets, 1962). A number of factors appear to influence vertical migration patterns in open ocean waters, including light intensity (Herman, 1963a, b; Bayne, 1964; Thoreson, 1964; Boden and Kampa, 1967; Hillier, 1970; Kampa, 1976), hydrostatic pressure (Lincoln, 1970, 1971; Ennis, 1973), salinity (Grindley, 1964), and temperature (McLaren, 1963). In addition, laboratory studies have considered the role of light and salinity as well as endogenous timing mechanisms as controlling factors in vertical migration (Lance, 1962; Bayne, 1964; Ringelberg, 1964; Enright and Hammer, 1967; Lincoln, 1970; Hughes, 1972; Group and Ellis, 1973; Ennis, 1973; Forward, 1974; Sulkin, 1975). The conclusion from studies using a wide array of techniques is that many mid- and deep-water plankton undergo rapid, extensive vertical movements on a daily basis.

The vital importance of planktonic components in ocean food chains has long been recognized. Vertical migration is of special interest in the study of energy flow in an ecosystem, since vertical displacement may markedly alter the availability of a component in the food chain.

Vertical migration studies have concentrated on open ocean waters. Only a few studies have considered estuarine waters where a relatively large number

of environmental factors may significantly affect water column movements of plankton (Carriker, 1951; Pinschmidt, 1963; Busch and Taylor, 1973; Sandifer, 1973; Hamuoto, 1975). Palmer (1974) studied vertical migration of benthic, intertidal forms. Carriker (1951) considered shallow water movement of bivalve larvae over two tidal cycles. As a consequence, only limited information is available on vertical movement of crab larvae in coastal marsh waters where they may be one of the dominant planktonic forms during the summer. Therefore, these experiments were carried out in the North Inlet Estuary to determine concentrations and patterns of distribution in relation to tides, light conditions and other environmental factors.

DISCUSSION

The data processed thus far suggest that the stage I zoeae are one of the predominant brachyuran planktors of the estuary. Furthermore, they appear to undergo a tide-related change in concentration as well as in distribution. The cyclic change in numbers could represent peaks of hatching of the young, and/or concentration of the zoeae at low tide in the main channel after being carried down from the headwater creeks. The resolution of this issue lies in careful studies of flushing rates and residence time in the estuarine waters (currently being carried out by D. Kjerfve), and by concurrent studies of larval concentrations at headwater, mid-channel, and outside the inlet mouth over several tidal cycles. The latter project has been too time-consuming to prove feasible.

The period of vertical movement, based on the present state of data analysis, appears to be tidal. Salinity changed very little in the water column during the sample period. Most other studies of vertical distribution in estuarine waters (Carriker, 1951; Pinschmidt, 1963; Busch and Taylor, 1973; Sandifer, 1973) concerned low-salinity, and may play an important role in upstream transport of larvae (Carriker, 1967). With the lack of a salinity gradient in the North Inlet Estuary, this factor is clearly of little importance; similarly, temperature plays little part.

Changes in distribution at the sample site, Old Man Creek in the North Inlet Estuary (Fig. 3), are not merely a function of laminar, differential flow rates in the water column. In the ebb channel, ebb flow rate reached a maximum during Tide Phase II, with relatively little difference in flow rate except for a few centimeters above the substrate (See Fig. 9 for graphical representation of the six phases of the tidal cycle). During Phase IV a slightly greater ebb flow occurred in the lower half of the water column but the rate overall was very low. Again, on the flood stages V and VI, the flow rate was relatively uniform from top to bottom of the water column. A large number of laboratory and field studies have suggested a role of light in the vertical movement of larvae (Cushing, 1951; Bainbridge, 1961; Herman, 1963 a, b; Bayne, 1964; Ringelberg, 1964; Thorson, 1964; Vervey, 1966; Braden and Kampa, 1967; Rudjakov, 1970; Lincoln, 1971; Forward, 1974; Kampa, 1976; Quinlin, 1975). Especially striking demonstrations of the effectiveness of light in depth regulation of zooplankton in the field have been studied during solar eclipses (summary in Kampa, 1976). Nevertheless, much remains to be discovered concerning phototactic responses at light intensities in estuarine and ocean waters. For example, the phototactic process itself may undergo endogenous rhythmic changes in Euglena (Bruce and Pittendrigh, 1958).

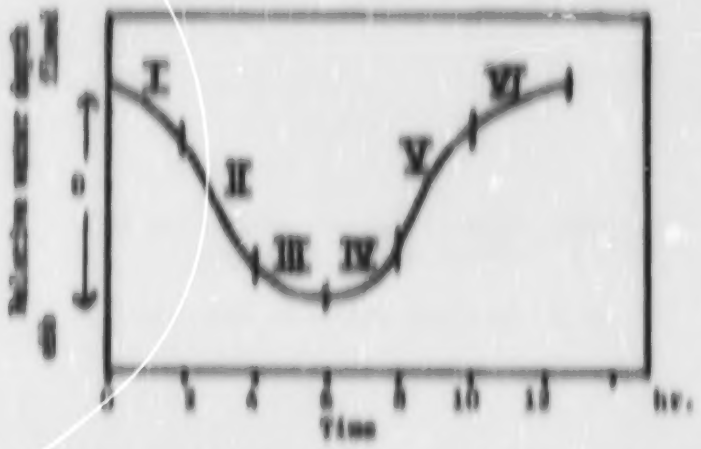

Figure 8. Sampling sites for 1974 vertical migration study (tide phases).

LIGHT, TIME OF DAY AND METABOLISM IN LARVAE OF *UCA PUGILATOR*

M. H. Vernberg and D. H. Jorgensen

INTRODUCTION

It has been well documented that many aspects of behavior of zooplanktonic larvae of marine organisms are controlled by light (Thorson, 1964; Herrnkind, 1968; Vernberg et al., 1973; Sulkin, 1975). Vertical migration of both larval and adult zooplankton, for example, is thought to be largely controlled by light (Bodon and Kampa, 1967; Bainbridge, 1961; Thorson, 1964). It also has been postulated (McLaren, 1963) that there is a link between vertical migration of marine animals and their metabolism. McLaren (1963) suggested that animals come to the surface waters to feed but, after feeding, descend to lower depths to conserve energy by reducing their metabolism at the lower temperatures found there. These studies indicate a possible link between vertical migration, metabolism and response to light. The present study was undertaken to measure the metabolic response of first-stage larvae of the fiddler crab, *Uca pugilator*, throughout a 24-hr period under different light regimes in an attempt to correlate metabolic response with light and with the vertical distribution of first-stage *U. pugilator* larvae observed in the field.

RESULTS AND DISCUSSION

In an experiment conducted under light-dark (LD) conditions (14 hrs light:10 hrs dark), the slowest rate of respiration was observed when light intensity was highest. This occurred at 1600 hrs when light intensity was 7.0 Joules/m^2/sec. As light intensity dropped, oxygen consumption rates decreased. Shortly after light intensity dropped to 0.9 J/m^2/sec, the metabolic rate increased, followed by a steady decline until the light intensity increased again at 0800 hrs. At that point, the metabolic rates began to increase again. The highest peak during the day occurred at 1000 hrs when light intensity was 3.1 J/m^2/sec.

Light intensities on the continuous light (LL) cycle remained high following 1600 hrs and oxygen consumption rates did not show the increase observed in larvae in the LD cycle. At 2300 hrs, when larvae on the LD cycle showed a sharp increase in respiration rate, the metabolic response of those exposed to the LL cycle decreased markedly; the response was a mirror

image of that observed for larvae in the LD cycle. After 2400 hrs, rates paralleled those of larvae in the LD cycle.

Bulkin (1975) demonstrated that responses to both light and gravity are used by crustacean larvae in depth regulation. He also noted that in one species, Leptodius floridanus, the larvae swim less actively when light intensity is high. Such a response would tend to position the larvae lower in the water column during the day when light intensity was highest.

It has been demonstrated in the laboratory that first-stage zoea of U. pugilator are highly photonactic at least during a part of the day (Vernberg et al., 1973). Data from the present study indicate that low light intensity has a very stimulating effect on respiration rates when it occurs following a period of exposure to bright light. Conversely, in the absence of darkness following exposure to bright light, respiration decreases sharply.

ENERGETICS OF ZOOPLANKTON

M. B. Vanmburg

Respiratory rates have been determined for the most commonly found species of adult zooplankton in the North Inlet Estuary and for three species of larval zooplankton. These data are summarized in Table 9. Data for meiofaunal species are given in Table 10.

Rates for both zooplankton and meiofauna were determined in Cartesian diver respirometers. Total volume of the divers was approximately 10 µl. Usually only one animal was used per diver, although with very small species it was necessary to use 2-4 for each determination.

These data are to be used in development of the energy flow model.

CONCLUSIONS

There are obvious species differences in the respiratory rates of zooplankton. Generally, oxygen uptake rates of larval zooplankton are lower than those of adult zooplankton. Respiration rates of meiofaunal adults also tend to be lower than those of the pelagic adult zooplankton. Since these are marked species differences, it is necessary to construct an energy budget for various species to understand their energetic role in the estuary.

TABLE 9. RESPIRATORY RATES OF ZOOPLANKTON FROM THE NORTH INLET ESTUARY.

	Temperature/Salinity	µls O_2/hr/mg dry wt
ADULT ZOOPLANKTON		
Parvocalanus crassirostris	25° - 30 °/oo	15.9 ± 1.0
Acartia tonsa[1]	15° - 25 °/oo	24.3 ± 1.3
Oithona brevicornis	25° - 30 °/oo	7.5 ± 0.8
Eurytemora affinis[2] (non-gravid Females)	Cold-acclimated (15°C)	
	15° - 30 °/oo	8.3 ± 0.9
	20° - 30 °/oo	14.1 ± 1.3
	25° - 30 °/oo	19.7 ± 2.0
	30° - 30 °/oo	22.5 ± 2.5
	Warm-acclimated (25°C)	
	15° - 30 °/oo	8.2 ± 0.8
	20° - 30 °/oo	8.8 ± 0.5
	25° - 30 °/oo	11.4 ± 0.7
	30° - 30 °/oo	9.8 ± 0.5
LARVAL ZOOPLANKTON		
Uca pugilator[3] Stage I	20° - 30 °/oo	4.0 ± 0.5
	25° - 30 °/oo	6.6 ± 0.5
	30° - 30 °/oo	3.9 ± 0.4
	20° - 20 °/oo	5.2 ± 0.5
	30° - 20 °/oo	4.6 ± 0.3
Stage III	25° - 30 °/oo	4.9 ± 0.2
	20° - 30 °/oo	4.8 ± 0.3
	30° - 20 °/oo	3.8 ± 0.2
Balanus balanoides Stage I	25° - 30 °/oo	12.5 ± 1.0
Stage IV	25° - 30 °/oo	21.7 ± 2.2
Cypris	25° - 30 °/oo	13.7 ± 0.8
Aequorius aequorius 1 day - Veligere	25° - 25 °/oo	6.4 ± 0.9
	15° - 25 °/oo	5.1 ± 0.7
7 day - Veligere	25° - 25 °/oo	9.4 ± 1.1

[1]Anderson, Gary. 1975.
[2]Vernberg, W. B. 1975.
[3]Vernberg, W.B. et al. 1975.

TABLE 10. RESPIRATORY RATES OF MEIOFAUNAL SPECIES FROM THE NORTH INLET ESTUARY.[3]

Species	Temperature/Salinity	µls O_2/hr/mg dry wt
COPEPODS		
Enhydrosoma leptoderma	25° - 30 °/°°	6.0 ± 0.6
Leptastacus macronyx	25° - 30 °/°°	7.5 ± 1.5
Scottolana canadensis	25° - 30 °/°°	6.0 ± 0.8
Nannopus palustris[1]	25° - 30 °/°°	7.2 ± 0.9
Thompsonula hyaenae[1]	25° - 30 °/°°	21.2 ± 1.7
KINORHYNCH		
Echinoderes sp.	25° - 30 °/°°	10.3 ± 0.9
TURBELLARIAN		
Pogaina sp.	25° - 30 °/°°	3.4 ± 0.2
CILIATE		
Tracheloraphis sp.[2]	25° - 30 °/°°	4.5 ± 0.3

[1]Heiner, B. W. 1976. (in press)

[2]Vernberg, W. B. and B. C. Coull. 1974.

[3]These data were obtained during a study under Grant BSO2938-02-0 from the National Science Foundation.

THE MACROBENTHIC FAUNA OF NORTH INLET: ABUNDANCE, DIVERSITY AND RESPIRATION

Richard Dame

INTRODUCTION

The benthic macrofauna are commonly members of the second and third trophic levels of most estuarine ecosystems and many species are economically important as food resources. Because of their trophic status, feeding methods and generally sessile existence, some benthic macrofauna may concentrate environmental pollutants such as heavy metals and pesticides, thus becoming pollutant indicators. In addition, some species of benthic macrofauna probably play important roles in cycles of nutrients and flow of energy.

North Inlet is typical of the small shallow, turbid estuaries in the southeastern United States. Because North Inlet is undisturbed, it is an ideal place to conduct base-line studies on an entire system. Benthic macrofauna undoubtedly form an integral component in such a system. There are two basic benthic environments common to North Inlet, intertidal and subtidal. The intertidal environments can be divided into salt marsh, oyster bars, mud flats and sand flats. The subtidal habitats are mainly sandy and muddy bottoms.

Previous and current work on the benthic macrofauna in North Inlet has been limited to the intertidal zone. Dame (1975, 1976) investigated energy flow in the intertidal oyster population, while Holland (1972) studies the population ecology of the clam Tagelus plebeius. Dame and Vernberg are studying the distribution and abundance of the snail Littorina irrorata, the fiddler crab Uca pugilator, and the crab Panopeus herbstii. In addition, Holland studied the animal-sediment relationships on the intertidal sand bars and mud flats.

Other studies of the macrobenthos of marsh-estuarine systems in the southeastern United States are taking place at Sapelo Island, Georgia and Beaufort, North Carolina. Early studies by the Georgia groups were directed at energy flow (Odum and Smalley, 1959; Smalley, 1960; Kuenzler, 1961; Teal, 1962). The Georgia studies have centered on carbon flux and nutrient cycling (Wiegert et al., 1975). The Beaufort studies have attacked a broad range of problems including energy flow and nutrient cycling (Wolf, 1975). These studies have recently concentrated on sea grass beds (Thayer, Wolf and Billiam, 1975; Thayer, Adams and LaCroix, 1975).

The major objective of the project is investigation and modeling of the functional and structural aspects of the system as a whole and not community analysis. To achieve this objective, the macrobenthic faunal studies of North Inlet have been and are being developed in three distinct phases. Phase I determined the distribution, abundance, biomass and diversity of the benthic macrofauna and is reported here. Phase II is currently in progress and determines the influences of the natural environment on various population and metabolic parameters. Phase III, not yet begun, will emphasize influences of environmental stress on major groups within the benthic macrofaunal component and how these stresses influence various components and the entire system.

DISCUSSION

The chemical-biological concept of benthic communities, as proposed by Petersen (1913), has been adapted by many workers to suit their projects. Marine biologists have traditionally recognized discrete communities or assemblages which existed in the North Inlet system and by sampling these selected areas over a long period.

The intertidal areas studied, Salicornia marsh, short Spartina marsh, tall Spartina marsh and oyster beds, are along an environmental gradient of decreasing elevation above mean low water or, in other words, decreasing stress due to exposure. The complexity of the macrofaunal assemblages of each of these areas showed the influence of exposure by decreasing the number of species and individuals per m^2. This agrees with many other investigations (Johnson, 1970; Holland and Dean, in press). The Fiddler crab Uca pugilator was the only organism common to the four intertidal habitats. While seasonal fluctuations in the number of organisms per m^2 of certain species were apparent (e.g., Nereis succinea and Crassostrea virginica), these fluctuations appear to be related to reproductive events and the influence of predators. Nereis succinea is common in the upper sediments and is known to become very active near the surface immediately after inundation by the tides. In the warmer months, North Inlet has a large resident population of birds, some of which commonly feed on macrofauna along the rising tide line. The number of young worms entering the populations was not studied during summer and winter because they are smaller than the 1-mm mesh of the sieve and thus pass through. It is not until winter that young worms have grown large enough to be found in the samples. The seasonal fluctuations of oyster numbers per m^2 was directly related to the July and August spatfall and has been discussed by Dame (1976).

Each of the five subtidal macrobenthic stations had a distinct faunal assemblage except at North Inlet mouth. The North Inlet mouth stations were in the main channel that empties the inlet and were exposed to the extreme stress of high flood and ebb currents. These currents are so strong that I believe no stable benthic community exists at this site and the organisms there are washed in from other areas.

The Jones Creek station (Fig. 1) is a sandy habitat (81% sand) and is numerically dominated by haustoriid amphipods. This compares well with

investigations of intertidal sandy habitats along the eastern U.S. where these animals also predominate (Holland and Dean, in press).

The Crab Haul Creek station (Fig. 2) was a muddy habitat dominated by many species also found in the intertidal oyster beds (16 out of 33 species found at Crab Haul station were also found in intertidal oyster beds). This might be expected since the habitats are adjacent. The major faunal difference was due to the ability of the oysters to survive extremely well in the nearby intertidal habitat thus increasing the developmental chances of the organisms living in this muddy zone.

The Debidue Creek mouth station (Fig. 2) was dominated by haustoriid amphipods also found at Jones Creek station, but an entirely different assemblage of polychaete worms was in evidence as well as a common predatory gastropod Terebra dislocata.

The last station was the Debidue Creek shelly site (Fig. 2) which had the most diverse assemblage of organisms of any sample site. This high diversity was mainly due to large numbers of tube-dwelling and burrowing polychaetes. The broken shells seemed to partition the environment and provide many habitats, allowing a highly diverse biological community.

Respiration studies that were begun are only a beginning in what seems to be a virtually unexplored area in the biology of southeastern estuaries. While many intertidal forms have been studied in detail (Teal, 1962; Vernberg, 1969; Dame, 1972; Holland, 1972) little is known about the functional aspects of most of the subtidal macrobenthic forms found.

The macrobenthic fauna are important in two components of the North Inlet system: the intertidal and the benthic subtidal. In order to facilitate the systems modeling aspect of the study, the standing crops of the yearly average biomass, respiration and production in kilocalories for the components indicated was calculated as follows. The caloric content of all organisms was assumed to be 5 kcal/g dry weight (Cummings, 1962). Yearly respiration was calculated using specific oxygen consumption found in our studies and data taken from the literature. Yearly respiration values for a given species in kcal/m^2/yr could be substituted into a relationship developed by McNeil and Lawton (1970) to predict annual production. Our values compare favorably with those estimates of Teal (1962) on a Georgia salt marsh. I know of no comparable work on subtidal estuarine macrobenthic fauna.

In conclusion, the macrobenthic fauna of the North Inlet system are both productive and important to the functioning of the system. The data gathered here is only a first step towards a more complete understanding of North Inlet as an undisturbed estuarine system.

DECOMPOSERS: MICROBIOLOGICAL STUDIES

L. Harold Stevenson and Gail M. Rubenbrecher

The microbiology group has been involved with measurement of two primary parameters within the estuarine system: decomposers (as indicated by ATP measurements of total microbial biomass) and water column detritus (as indicated by particulate organic carbon). In addition, several secondary factors, i.e., current, depth, suspended solids, heterotrophic bacteria, dissolved oxygen, etc., have also been measured. The assay of these parameters within the type of environment to be modeled presents several unique problems. A salt marsh is not a homogeneous environment. Individual creeks differ one from another and their overlying water masses also differ. The rise and fall of the tides present an additional complicating factor.

Tidal flux has been shown to influence the distribution and ecology of many estuarine plants and animals. Yet, the effect of tides on estuarine microorganisms in the water has received little attention. Some data on the numbers of aerobic, heterotrophic bacteria in coastal waters are available (ZoBell, 1946; Stevenson et al., 1974). Other studies have focused on such topics as the tidal transport of detritus (Odum and de la Cruz, 1967), the distribution of nutrients in estuarine (Leach, 1971), coastal (Alexander et al., 1973), and swamp waters (Walsh, 1967), the activity of microorganisms over a tidal cycle (Morita et al., 1973), and the enumeration of sediment microflora and grain size distribution (Krumbein, 1971). A major portion of the work, therefore, was initiated to measure the influence of tides on the concentration of the microflora in the water column.

The investigation of the estuarine system has progressed through several phases of increasing complexity. They include: 1) monitoring two small tidal creeks over 12-hr tidal cycles, 2) statistical analysis of the 12-hr data, 3) survey data from several creek stations throughout the marsh, 4) monitoring marsh creeks of increasing size over 40-hr sampling periods, and 5) analysis of sediments.

The first phase consisted of a comparison of two marsh creeks. Station 1 was located at the entrance to a small, intertidal creek that drained 4 hectares of *Spartina* marsh and had a soft, silty-clay bottom. Salinity during the sampling periods ranged from 15 to 34 o/oo. The maximum number of bacteria per ml of water was reached just prior to low tide and appeared to be associated with the resuspension of sediment since

increase in the turbidity of the water at Station 1 was frequently encountered at low tide. The slightest wind disturbance of the shallow water resulted in suspension of the soft sediment. The average number of bacteria over the complete tidal cycle was 2.18×10^9/ml. The concentrations of particulate organic carbon (POC) and ATP likewise changed over the tidal cycle with POC at low tide (8.10 g/m^3). Although the increased turbidity of the water near low tide did not result in a substantial discontinuity of the POC data, the concentration of ATP did reflect this disturbance. Prior to low tide, the concentration of ATP rose about 9-fold to a maximum of 3.53 mg/m^3.

Station 2 (Fig. 2) monitored a creek that drained 13 ha of marsh and about 170 ha of pine forest. The creek had a firm sandy bottom and measured 13 m across at the sampling site. Salinity ranged from 2 to 34 o/oo during the sampling periods. The highest number of bacteria per ml of water occurred just prior to low tide and then declined on a rising tide. The average number of bacteria over the tidal cycle was 1.73×10^8/ml and was an order of magnitude lower than that reported for Station 1 over a similar tidal cycle. Maximum POC was observed just prior to low tide; this concentration was about three times greater than that at high tide. The mean concentration of POC, 1.69 g/m^3, was less than half that observed at Station 1. The concentration of ATP in the water progressively increased from a minimum value of 0.33 mg/m^3 at high tide to a maximum value of 1.82 mg m^3 at low tide. The mean concentration of ATP over the tidal cycle (1.01 mg/m^3) was not significantly different from the mean concentration reported for Station 1. Additional tidal studies of both marsh creeks confirmed these earlier observations. In all cases, maximum and minimum values occurred at or near low tide and high tide, respectively. In general, the concentrations of ATP and POC were greater at Station 1 for the same sampling periods. Bacterial numbers, on the other hand, were consistently higher at Station 2.

The second phase of the study consisted of an extensive statistical analysis of the relationships between the physical-chemical parameters and the biological components of the water column. Emphasis was placed on the distinction between ebb and flood water masses. There was significant (0.05 level) Pearson correlation coefficients between all of the biological components (ATP, bacteria, and POC). Likewise, there were significant correlations between salinity and water level and the biological parameters. The flood tide data lacked most of the significant linear relationships observed for ebb tide data. The interaction between the biological components all but disappeared except for ATP with bacteria.

The third phase of the investigation involved sampling a total of eight stations at points throughout the system from 1973 to 1975. More complete data are available on four locations of increasing complexity: Clambank, Oyster Landing, Old Man Creek, and North Inlet. Mean data for detritus-carbon (POC) decreased with increasing size of the creek (1662 mg/m^3 at Clambank to 850 mg/m^3 at North Inlet); while biomass carbon was more abundant in the two larger creeks than the small systems (about 400 mg/m^3 vers 300 mg/m^3).

Several long-duration studies of the amounts of microbial biomass and detritus in the water column of Oyster Landing Creek comprised the fourth section of the study. Each study period included hourly sampling through at least three high tides and three low tides. The previous observations, that the biological parameters were minimal at high tide while highest values were recorded at low tide, were confirmed. However, consecutive tidal cycles demonstrated marked differences in the values recorded. Transport values calculated in conjunction with these studies indicated that the marsh environment studied was generally an exporting system which consistently (but not always) lost more detritus and biomass on a falling tide than was imported on a rising tide.

Limited data are available on the fifth segment of the work -- biomass measurements in sediments. Preliminary information indicates that the interface zone in the high marsh between the forest and the Spartina-area contains highest levels of detritus carbon (10 mg/g) and biomass carbon (4 mg/g).

There are two significant points in addition to a direct interpretation of the results. These relate to station location and sampling schedules. The data indicate that marked differences were found among various stations. The values obtained were directly influenced by location of station. The selection of one or a few stations and considering them to be indicative of the entire marsh cannot be done. Likewise, critical differences were observed among data collected on the various sampling dates and, perhaps more importantly, between consecutive tidal cycles. The selection of a single cycle or a single sampling time as representative of a longer period, i.e., a month, is not valid.

RADIATION BALANCE IN THE NORTH INLET MARSH

Sterling J. Crabtree and Bjorn Kjerfve

INTRODUCTION

Radiant energy received by the earth's surface is primarily composed of short-wave (~0.5 μm) radiation from the sun and long-wave (~12 μm) radiation from the atmosphere. This radiant energy is either absorbed by the earth or reflected. The absorbed radiation heats the surface, which reradiates long-wave energy. The difference between incoming radiation and outgoing radiation is called net radiation and is a measure of the energy available at the earth-atmosphere interface at a given site for heating of water, soil and air, and for evaporation and photosynthesis.

The radiation balance has been studied by a number of investigators over a wide variety of natural and agricultural surfaces (Monteith and Szeicz, 1961; 1962; Ohern, 1965; Stanhill et al., 1966; Polsvarapu, 1970). Most investigators have used only data obtained on clear days in determining relationships between net radiation and total incoming radiation. We show that a linear relationship exists between net and incoming radiation for a Spartina marsh site at North Inlet, not only on sunny days, but also on partly cloudy days if the radiation data are numerically smoothed to remove random short term variability.

Monteith and Szeicz (1961, 1962) showed that the radiative characteristics of agricultural surfaces can be described by the linear regression equation

$$Q_n = Q_s(1 - a)/(1 + \beta) + L_u \qquad (1)$$

where Q_n = net radiation integrated over all wavelengths
Q_s = total short-wave radiation from the sun and sky
a = albedo or reflection coefficient of the surface
$Q_s(1 - a)$ = net short-wave radiation
β = heating coefficient
L_u = balance of long-wave radiation between the surface and atmosphere

Studies by Davies (1967) and Ohern (1965) have shown that the totals of net radiation, Q_n, for daytime conditions can be expressed as a function of the total solar radiation, Q_t where a is the axis intercept and b is the

slope of the regression line, the regression coefficient, is a simpler form

$$Q_N = bQ_g + a \qquad (2)$$

with a correlation coefficient better than 0.9 (Davies, 1967).

From equations (1) and (2), it follows that the regression coefficient, b, is given by $b = (1 - \alpha)/(1 + \beta)$. Monteith and Szeicz (1962) found that α and β were equally important in determining Q_N. On the other hand, Stanhill et al. (1966) concluded that β and L_g varied only slightly for different surfaces while α affected Q_N the most (Davies, 1967).

RESULTS AND DISCUSSION

Instruments were placed on two adjoining sites in a 1-m high *Spartina alterniflora* salt marsh at North Inlet between 6-9 July 1974. All data were recorded as analog traces on strip charts and digitized with a 10-min sampling rate on a Bendix Datagrid digitizer. In the following analyses we used only data points measured during daylight.

Since the two sites were separated by 200 m, all data were filtered to remove data noise generated by differential cloud passages and other high frequency phenomena. We chose a second order, recursive, Butterworth low-pass digital filter (Ackroyd, 1973) after considerable experimentation.

After filtering, we computed the daily means and standard deviations of net, solar, and reflected radiation.

Linear regression of net radiation, Q_N, on solar radiation, Q_g, yielded

$$Q_N = 0.72\ Q_g - 9.5 \qquad (3)$$

with a correlation coefficient $r = 0.99$, where Q_N and Q_g are measured in W m^{-2}. Equation (3) is in fair agreement with the relationship found by Ebern (1965) for a sugar cane field in Hawaii. His regression coefficient is 0.81 and $L_g = -105$ W m^{-2}.

Equation (3) applies to summer conditions for clear to moderately cloudy days. Most afternoons, thunder showers passed over North Inlet, reducing the total amount of incoming radiation. The daily average of total solar radiation was 380 ly (15.9×10^6 J m^{-2}) as compared to 750 ly for total solar radiation received on clear summer days on Hawaii (Ebern, 1965). Ebern's regression fit included only data from clear days, which explains his higher L_g value as compared to our analysis. In agreement with Davies (1967), the strength of Equation (3), however, is that it shows an excellent fit to typical North Inlet July conditions with a considerable fair-weather cumulus cloud cover and occasional thundershowers.

Comparison of net radiation to incoming radiation for the 6-day period indicates that Q_N on the average amounts to 69% of the incoming radiation. Ekern (1965) listed the Q_N-percentages for a variety of surfaces between latitudes 56°N and 19°N. The summer values ranged from a low of 41% above grass sod in England to a high of 59% above sugar cane in Hawaii. Sugar cane has a primary production rate greater than Spartina alterniflora.

The albedo, a, was computed as the ratio of total reflected radiation to total solar radiation for each day and allowed the calculation of daily heating coefficients, β. Whereas a is fairly constant coefficient of variation (c.v. = 16%), β and L_u both vary considerably (c.v. = 61 and 76%, respectively) and therefore control Q_N. This is in disagreement with previous studies, but is probably due to day-to-day variations in cloud cover, which greatly affects the long-wave radiation balance. Other studies have usually only treated conditions on clear days.

Further, it is desirable to be able to estimate the reflected irradiance from measurements of Q_N to enable albedo computations. We regressed Q_R on Q_N and found

$$Q_R = 0.079\ Q_N + 3.4 \qquad (4)$$

with r = 0.94, using all 495 filtered data points. As $Q_N > Q_R$ it is obvious that the relationship is not valid for very low values of solar radiation. The analysis implies a mean summer albedo of 0.09 for the S. alterniflora marsh. It also shows a slowly decreasing albedo for higher values of Q_N as can be expected with a greater solar elevation. In comparison, Ekern (1965) reported a range of albedos in Hawaii from 0.05 for lava to 0.15 for cane, whereas Monteith and Szeicz (1961) computed a 0.26 albedo for grass in England. Our low albedo may be explained, considering that the reflected radiation is an area-composite value including Spartina plants and the underlying, dark mud surface.

In summary, the empirical relationships, Equations (3) and (4), enable direct computation of net and reflected radiation from a pyranometer record for typical July conditions in a South Carolina Spartina marsh. Whereas Q_N and Q_R seldom are measured directly in spite of their wide variations with the underlying surface, Q_S is measured routinely at most meteorological instrument sites.

HYDROGRAPHY OF NORTH INLET, SOUTH CAROLINA

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North Inlet belongs to a class of coastal plain estuaries which has received only limited attention by physical oceanographers. An extensive field investigation in 1974 resulted in 947 vertical profiles of velocity, temperature, salinity, and σ_T at 20 stations. During 1975 an additional 1,100 profiles were measured. Tidal elevation, atmospheric pressure, and wind speed and direction were recorded continuously at one location. During the perigee-syzygy tide in February 1974 the 300 km^2 estuary-marsh system experienced a maximum 2.4 m tidal range and 140 cm/sec currents. Neap tides are characterized by a 1.0 m tidal range and maximum currents of 80 cm/sec. Gravitational circulation is extremely weak as fresh water is primarily derived from local rainfall. However, during periods of high discharge of the Pee-Dee River into Winyah Bay, fresh water spills into North Inlet, primarily through Jones Creek, increasing the gravitational circulation. The net, depth-mean flow, averaged over the 20 stations, was 6.9 cm/sec in the ebb-direction during high run-off conditions compared to 1.9 cm/sec ebb flow during low run-off. Similarly, salinity was 33.1 o/oo and 34.4 o/oo, respectively. Tidal pumping appears to be the dominant circulation mode with net ebb currents in the main channels and net flood currents in the secondary channels. Weather systems commonly cause mean sea level in the estuary to oscillate as much as 80 cm with a typical period of 5-7 days. With respect to density, North Inlet is vertically and horizontally homogeneous, but time-variations of σ_T are highly significant. North Inlet is a class 1a estuary (Hansen and Rattray, 1966) during high and low run-off with a circulation parameter on the order of 1 and a stratification parameter on the order of 10^{-3}. Simultaneous tide measurements at the North Inlet stations over a 3-week period indicated that the tide may be approximated by a frictional progressive wave. Extensive bathymetric measurements indicated that net circulation patterns in this kind of estuary may be induced from cross-sectional channel shapes and the longitudinal orientation of sand waves.

FIELD MEASUREMENTS

Current speed and direction, conductivity, and temperature were measured at 20 stations in the North Inlet estuary at one-meter intervals from surface to bottom. Water elevation, wind speed and direction, and atmospheric pressure were recorded continuously at one station. Bottom

morphology was determined for a large number of cross sections and some longitudinal sections throughout the system.

PRELIMINARY CIRCULATION RESULTS

During the perigean-syzygy February tide in 1974, tidal currents reached a maximum of 140 cm/sec; the maximum tidal range was 331 cm; net currents in places reached 36 cm/sec, directed toward the inlet. This field study coincided with high run-off through Winyah Bay (Fig. 2) with some flow-through into the North Inlet system.

During the October neap tide, tidal currents reached no greater speeds than 94 cm/sec; the tidal range was as low as 110 cm; and the net velocities were typically below 10 cm/sec. The run-off in Winyah Bay was low at this time and no inflow from Winyah Bay was noticed.

North Inlet is a homogeneous estuary with respect to density, salinity, and temperature. A three-way analysis of variance, replicating on station, tidal stage, and depth, indicated that only the stage accounts for a highly significant amount of variation and with a significant amount of variation due to station location. Interaction terms and variations due to depth were insignificant. Therefore, a one-dimensional numerical model could successfully be used to model the North Inlet circulation.

The gravitational circulation is weak but noticeable during high run-off through Winyah Bay. The most important circulation mode seems to be a pumping circulation: net velocities are directed oppositely in the same cross section, pointing to a Class C estuarine type (Pritchard, 1955), where lateral circulation is the main feature.

North Inlet may best be classified as a type IA estuary (Hansen and Rattray, 1966). It appears that this can be expected of most southeastern marsh-estuary complexes (Kjerfve and Ivester, 1974). These estuaries are characterized by low values of the circulation and stratification parameters and have not previously been described with respect to the physical oceanography.

BATHYMETRY AS AN INDICATION OF CIRCULATION

Net ebb-directed currents were found in the deep channels of Town Creek, Old Man Creek, and North Inlet (Fig. 2), whereas net flood flow was measured in the secondary channels in the same cross sections. Extensive longitudinal fathometer traces were made during flood and ebb tides, showing the existence of ebb-oriented sand waves (approximate height 0.6 m; approximate wavelength 20 m) and flood-oriented sand waves in the secondary channels.

The implication is that net circulation patterns possibly could be determined from bathymetry measurements alone in shallow estuaries similar to North Inlet (Kjerfve, 1975).

DISCHARGE COMPUTATIONS

The tidal prism for North Inlet, as determined from velocity measurements varied from 47 x $10^6/m^3$ for neap to 106 x $10^6/m^3$ for spring tides. The intertidal volume fraction was then approximately equal to the mean estuarine volume during spring tide but only 0.45 of that volume for neap tide.

The maximum discharge through the North Inlet section consistently occurred during the first half of the falling tide. The maximum ebbing discharge then exceeded 2,200 m^3/sec. Maximum flood discharge occurred during the middle of the falling tide, with a maximum discharge below 1,500 m^3/sec.

The time-averaged or net discharge through the same cross section was typically on the order to 20 m^3/sec but in extreme cases exceeded 100 m^3/sec. This happened during the February 1974 study.

The time-averaged exchange between North Inlet and Winyah Bay primarily seemed to take place through Jones Creek. However, the direction of exchange varied. An appreciable net discharge occurred during the February 1974 study from Winyah Bay into North Inlet. The net discharge was then estimated to be approximately 60 m^3/sec. However, during the neap tide study in October 1974, net flow, as measured at a cross section, was 7 m^3/sec directed from North Inlet to Winyah Bay.

WATER LEVEL SPECTRA

Finite Fourier transforms were carried out on 3 simultaneous 20-day water level records. The records were digitized with a sampling rate of 1 hr. The semi-diurnal tidal peak completely dominated each spectrum. However, the diurnal peaks were also easily recognized. There also existed a dominant peak in the ocean gauge record at a period of 3.2 days, which probably is associated with passages of weather systems.

Cross-spectral analysis indicated a lag of 41 min for the semi-diurnal tide wave at Clambank Creek (Fig. 2) relative to the ocean gauge. This lag time was 4-5 times longer than what could be expected from a frictionless shallow water wave. The phase relationship between currents and water level fluctuations indicated that the North Inlet tide may have been of the standing type. However, Hunt (1964) pointed out that a frictional, progressive wave may exhibit the same current-tide phase relationship as a standing wave. Therefore, in modeling the North Inlet tide, it will be necessary to include friction in order to simulate the tidal behavior successfully.

DATA RETRIEVAL SYSTEM

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A modeling oriented research project requires good field data for model calibration. The present study has focused on collecting physical time series data from the North Inlet Estuary. These data have been incorporated into an easily accessible computer disk storage system.

The completed data set consists of four variables: 1) water elevation at Clambank Creek (Fig. 2), relative to existing NOAA bench marks; 2) wind speed at an elevation of 15 m at Clambank; 3) wind direction at Clambank; and 4) atmospheric pressure at Clambank. The variables have been recorded by means of a WeatherMeasure P551 water elevation gauge for the tide, a Climet (Climet Instrument Co., Redlands, CA) CI-26 recording wind system with a two-channel Easterline Angus recorder for the wind speed and direction, and a WeatherMeasure B211 microbarograph for the atmospheric pressure.

Each instrument was installed in late April 1974, and has given a continuous time series. This has required constant checking of instrument operation and calibration. We have serviced the instruments on at least a weekly basis since installation. With respect to the tide gauge, this included a monthly relevelling of the baseline relative to existing bench marks to insure against bias errors.

Each analog record trace was prepared in the office. Field time checks were converted to Eastern Standard Time (EST) and coded according to Time-Day-Month-Year: e.g., 2015-01-02-75 would mean 8:15 p.m. on 1 February 1975.

Each time series was digitized using an existing Bendix Datagrid Digitizer. The analog records were converted to information on electromagnetic tape. Through an elaborate FORTRAN program, the tape information was sampled at 10-min intervals on the hour and each 10-min clock increment. Corrections were made for non-linear instrument chart-paper feeding, curve-linear recording pens, and sloppy digitizing procedures. The sampled data points were punched on computer cards. These cards were hand-edited, insuring correspondence between recorded signals and punched data points.

In the next step, these edited data points were stored on a direct-access disk, available through the University of South Carolina Computer Services Division IBM 370/168 system. The total data set presently consists

of one complete year, beginning at 0000 1 June 1974 and ending at 2350 31 May 1975. The sample rate is 10 min and each one of the four series consists of 52,560 data points. A variable pointer, IR, can be set to an arbitrary hour value subsequent to the IR=1, the beginning of the series. However, IR must be less than 8,760, the total number of data hours. Thus it is possible to access the entire set or only a portion thereof, depending on the particular application. The FORTRAN IV program, which runs in class B in less than 2 min CPU time, may be used to access the data set.

The Eppley pyranometer located 100 m south of the Baruch coastal laboratory in a California marsh plot has yielded continuous records of total incoming solar radiation for two years. Portions of this record have been digitized and processed in a manner similar to the other four parameters. However, extensive statistical calibration of these data compared to several other similar instruments erected next to the pyranometer indicates extensive data inconsistencies. The reason appears to be poor maintenance of the pyranometer cell: paint flaked from the sensor unit and salt and dust spray covered the hemispherical sensor dome for extended time periods. For these reasons, we decided not to store the 1974–75 radiation data on the data disk along with the tide, wind, and pressure records.

SALT MARSH UNIT MICROECOSYSTEMS FOR ASSESSMENT OF POLLUTANT ADDITION PERTURBATIONS

Miley Kitchens

INTRODUCTION

Detailed studies of the coastal ecosystems (Odum and Smalley, 1959; Smalley, 1959; Pomeroy, 1959) have led to a general awareness of the intrinsic value of the Spartina alterniflora salt marsh community to the coastal systems through its various supportive roles, such as (1) an ultimate source of carbon and other nutrients to the complex marine food webs, (2) a primary nursery ground for the coastal fisheries, providing both food and harborage to larval and juvenile stages of various species, and (3) a stabilizing force retarding coastal erosional processes. Further studies have detailed aspects of community structure, energy flow, and material fluxes through the marsh system (Teal, 1962; Odum and de la Cruz, 1967; Day et al., 1973). To date, however, the only substantive data available regarding environmental alterations are the studies of Chapman (1960) and Schmidt (1966) detailing the effects of dredging and filling operations and Valiela et al. (in press) detailing the effects of sewage applications.

The microecosystem or "microcosm" approach is a logical way to experimentally assess whole community responses in terms of sensitivity or susceptibility to additions of real or potential pollutants under controlled conditions. This approach has been successfully employed to investigate aspects of such fundamental ecosystem processes as nutrient cycling in aquatic systems (Whittaker, 1961), patterns of community metabolism (Beyers, 1963, 1965), patterns of ecological succession under various environmental regimes and stresses (Cooke, 1967; Wilhm and Long, 1969; Kitchens, unpublished data), response to low freshwater flow regimes in estuaries (Cooper, 1970), and associated community responses to environmental alterations in flowing streams (Odum and Hoskin, 1957; Revern and Ball, 1969; Lauff and Cummings, 1964; McIntire et al., 1964). Odum and Chestnut (1970) reported ecological systems that developed when the treated waste from municipal sewage systems flowed into estuarine waters.

One obvious advantage to the microecosystem approach is that the test pollutants are not released into a natural ecosystem if a treatment system is attached to it. This can be a critical factor in heavy metals and pesticide studies. Other advantages are (Beyers, 1963): (1) some control of boundary conditions so that variations can be attributed to the responses

under investigation, (2) ease of replication for statistical analyses and modeling, (3) study of systems small enough to control, but large enough to maintain complexity, (4) sacrifice of units at given intervals, so that random errors will be independent of random error in other experiments, and (5) the test pollutants are not directly released into the natural ecosystem; they can be managed and/or controlled.

This study has and is currently being conducted in several phases. The initial phase was the period during which the microecosystem marsh units were being designed and constructed. The second phase was testing and evaluation of the replicability of the units for various critical responses. The third phase will be the perturbation phase during which replicate microecosystem units will be manipulated by pollutant additions and compared with unperturbated control units for assessment of effects of pollutant additions.

The community metabolism response was selected for several reasons: (1) it has been shown to be a sensitive indicator of community imbalances in various aquatic systems (Copeland and Dorris, 1963; Copeland, 1965, 1967), (2) replicate laboratory aquatic systems do not differ significantly with respect to rates of community metabolism (Abbott, 1956), and (3) ease of automation for measurement of response.

Other measurements of either community structure or physiology have been used as time permitted to determine the validity of the community metabolism response and calibrate the test against the natural marshes.

The specific aims of this work are: (1) to determine and demonstrate the general utility and universal application of the microecosystem technique for pollution studies at various marine laboratories, (2) to develop several predictive and simulative models for various potential pollutants threatening coastal marshes, and (3) to test the validity of the general ecosystem model for the North Inlet area by direct measurements as well as contribute data to that model.

DESCRIPTION OF EXPERIMENTAL TANKS

The units were designed essentially as combination "containerized" short Spartina alterniflora salt marsh plots and metabolism chambers. The following sections will outline and detail construction and sampling procedures.

Construction of the Combination Holding Tanks and Metabolism Chambers

Tank Fabrication--

Four replicate square tanks (8' x 8' x 1.5') were fabricated from rigid sheets of PVC. The tanks were constructed to serve dually as a holding tank for miniaturized salt-marsh plots (with attendant floral and faunal communities) and gas analysis chambers for measurement of community metabolism. Each unit also is fitted with an airtight plexiglas lid for sealing tank

atmospheres for gas analysis. During normal operation the tanks are left open to the atmosphere and are flooded and drained twice daily in synchronization with the local tides.

Marsh Plots--

Each of the tanks was seeded with plots of *Spartina alterniflora* salt marsh (1 ft^2 in area) with substrate intact to a depth of 6 inches. These plots were transplanted from the local marsh during the first two weeks of January, 1975. It was hoped that the trauma of transplantation would be minimized during this rather dormant period for both the *Spartina* and the invertebrate benthic fauna within the substrate. The following photographs depict layout of the units as well as some close-ups of the marsh plots. New growth of the *Spartina* was observed along with increased activity among the infaunal and epifaunal communities within the ponds in the eight months since transplantation. Oysters have been placed upon racks within the screening box at the effluent water drain end of each tank. Growth studies will be initiated as a further test of system replicability.

Overview of tanks (with lids in place) depicting the layout of some of the plumbing and the marsh plots.

Within tank view of the transplanted marsh (note shoots).

Tidal Sea Water System--

Water from a creek adjacent to the transplant area in the marsh is pumped into the units upon signal from a set of remote timers. The period between successive high tides is 12.45 hours and is reset on occasion to approximate tidal conditions in the local marsh. The system has been

operating as a flowthrough system. However, it is adapted for the inclusion of a 900 gallon capacity storage tank to operate on a closed system for units exposed to pollutants. The pools are filled at a rate of 9.4 l/min and drained at a rate of 2.4 l/min. The water attains a level of 6 inches over the base of the marsh plants within the 2-hr filling period.

Gas Analysis System--

The gas sampling and analysis system for each of the tanks is now complete. The system is composed of: 1) an interval timer, 2) flow meters, 3) tubing (polyethylene), 4) pumps, 5) PVC needle valves, 6) infrared CO_2 analyser, and 7) a digital data recorder. The system is designed to permit either flowthrough or closed circulation analytical sampling techniques. We have employed the integration of CO_2 concentration rates of change curves as described in Odum and Hoskins (1958) for oxygen concentration (modified for CO_2 in our study). Prior to the analysis (CO_2 concentration determinations) each of the tanks is sealed with a transparent plexiglas lid. The lid is composed of two 4' x 8' sheets of 1/4" plexiglas and PVC supports. When fitted in place the lid seals the tank to the atmosphere and forms a fixed inside chamber volume. Samples of the atmospheres within the tanks are pumped to the gas analysis equipment by remote signal timers, pumps, and solenoid valves. CO_2 flux is monitored during a 24-hr period at hourly intervals in each of the tanks. From these data, net photosynthesis and respiration rates are determined.

Temperature Control System--

An air conditioning system for temperature regulation was installed in each of the tank units to prevent heat buildup due to a greenhouse effect. This system consists of an individual 7800 BTU air conditioner for each tank. The units share a common control system designed to keep the temperature within the tanks within 3°F of the ambient atmosphere. The control relay regulating the temperature is activated by differential internal refrigerant pressures within the inside and outside temperature sensors.

Nutrient Flux Determinations

Nutrient flux rates into and out of each of the units were determined utilizing concentration of the various constituents and discharge measurements for the tidal waters into and out of each of the units. The following determinations were made for a sampling period at 30 min intervals: 1) reactive phosphorous, 2) total phosphorous, 3) ammonia nitrogen, 4) nitrite nitrogen, 5) nitrate nitrogen, 6) total nitrogen.

Community Structure Analyses

The benthic communities in each of the units was subsampled by extracting a 10 cm^2 core the depth of the substratum. Ten replicates were taken from each of the units and sacrificed and analysed for macrobenthos by the technique of Dame (see Macrobenthos section). A replacement core from the natural marsh was substituted for the removed core sample.

Microbial biomass determinations will be made on a quarterly basis utilizing the technique of Stevenson (see Microbiology section).

RESULTS

In summary, we have found good agreement among the four replicates both primary productivity and nutrient budget studies. Although the studies are still in the preliminary stages, we have observed rather consistent trends in the ratio of net photosynthesis to nighttime respiratory values. For our first three preliminary sample runs, the values have been just slightly less than 1 or unity. Our preliminary nutrient budget indicates importing of total phosphorus and exporting total nitrogen. This pattern has been noted for our first two sample runs with good agreement among replicates for each run.

The benthic community faunal survey at this point is still incomplete. Initial data indicate a lower species diversity in the tank units that at the sample site for the natural marsh. We feel this may indicate a drainage problem in the units and will follow the results of this study closely, preparing to make some alterations to improve drainage if necessary.

SECTION 6

SUMMARY OF REPORT

F. J. Vernberg

This report represents the results of the first two years of what was designed as a five-year project. To understand the dynamics of a relatively undisturbed marsh-estuarine ecosystem, the North Inlet Estuary, Georgetown, S. C. both macroecosystem and microecosystem approaches were used. The two principal objectives of this macroecosystem study were: 1) to establish baseline data on an undisturbed estuary to provide a scientific basis for comparative studies on the effects of various stresses of pollutants or other estuarine environments; and 2) to develop models of an estuarine ecosystem which would predict the probable effects of environmental perturbation. The principal objectives of the microecosystem were: 1) to develop and test replicate experimental salt marsh units at the microecosystem level as diagnostic tools for the assessment of both long- and short-term pollution effects on the *Spartina alterniflora* salt marsh community; and 2) since this study was conducted in conjunction with the ecosystem analysis of North Inlet Estuary, these simulated marshes will be utilized to test, as well as to provide some data relevant to the general overall ecosystem model being constructed for the area.

During the initial phase of this five-year study, specific substudies were started and the study of other key processes were to be investigated in subsequent years. Therefore, in keeping with the experimental design of the project, only those substudies are discussed and a comprehensive analysis of the marsh-estuarine ecosystem cannot be presented at this time.

Field studies involving 10 faculty and postdoctoral investigators and modeling procedures were initiated simultaneously.

A comprehensive conceptual energy flow model has been formulated which consists of three distinct subsystems: water column, intertidal marsh zone, and the benthic subtidal zone. A linear dynamics system with 22 states was chosen as the mathematical model. A "first attempt" dynamic model for the water column submodel has been formulated mathematically and a simulation program constructed. Additional field work, which was proposed as part of the original experimental design, is needed to evaluate various system parameters.

In addition, a linear systems model of the intertidal oyster community was developed. Simulation of the mathematical model indicated that the

original model was near stability. This result agrees with those of a five-year field study of oysters. A 1^{st} sensitivity analysis of the parameters in the mathematical model affords some order in which these parameters should be studied.

PRIMARY PRODUCERS

The aboveground production of halophytes in North Inlet, mainly Spartina alterniflora, has been estimated as about 900 g/m^2/hr. Considering the productivity data reported here, the phytoplankton, together with the benthic microflora, produced about the equivalent amounts of carbon per year as the halophytes. Since the "mufwuche" community, the benthic macroalgae and the surface film community are not considered, it appears that in North Inlet, the algae are the more important primary producers. If this is true, then our concepts regarding the relative ecological significances of the various plant communities in salt marsh estuaries must be revised. At the very least, algae must be considered as an important trophic compartment in our model of the North Inlet Ecosystem.

ZOOPLANKTON

The zooplankton of the North Inlet Estuary were collected bi-weekly from January 1974 to August 1975 at four stations. Zooplankton numbers ranged from 177 to 84,414/m^3 ($\bar{X}$=9,234/m^3) and biomass from 640 to 140,169 µg dry weight/m^3 ($\bar{X}$=16,009 µg dry weight/m^3). The major peak in the density of zooplankton occurred between April-July both years.

Copepods (including larval stages) were the most dominant taxon comprising 64-69% of total zooplankton numbers and biomass. The most common species were Paracalanus crassirostris Dahl, Acartia tonsa Dana, Oithona colcarva Bowman and Eutorpina acutifrons (Dana). Cirripedia nauplii were the most common meroplankters, comprising 13% of the total zooplankton for the entire sampling period. Other important groups were bivalve and polychaete larvae and Oikopleura sp. Comparisons of the major species of copepods and their reproductive periodicities with those reported in the literature suggests that the North Inlet Fauna is most closely allied to that of Florida waters.

The analysis of zooplankton vertical migration was undertaken to establish both a basis for estimating standing crop and an understanding of the role of environment fluctuation on species dispersal. Uca spp., predominant brachyuran planktors, were found to undergo regular changes in numbers and vertical position in the water column. Maximum numbers were found at the time of low and rising tides and a concentration in the lower quarter of the water column occurred at these times.

Laboratory estimates of the energetics of various zooplankton species were determined under combinations of temperature and salinity. These data will be used in the development of the energy flow model.

MACROBENTHIC FAUNA

Data on the macrobenthic fauna for model development in the following subject areas were analyzed: abundance, diversity, and respiration. These data were collected on a phasic experimental design. The first phase dealt with distribution, abundance, biomass and diversity of the benthic macrofauna. The second, which was initiated the second year, involved a study of the influence of natural environmental factors on populations and metabolic responses. The next phase, not yet begun, will emphasize the influence of environmental stress, including pollutants, on the benthic macrofauna.

DECOMPOSERS

The role of decomposers was studied in phases. Numbers of decomposers and amount of water column detritus were determined. Initially, the smaller tidal creeks were monitored over a 12-hr tidal cycle. This was followed by statistical analysis of the relationship among the physical-chemical parameters and biological components of the water column using an IBM-370 computer and the SPSS and SAS statistical packages. The monitoring program was expanded to include larger creeks over a 40-hr sampling period. These data were needed for estimation of energy flow dynamics.

SOLAR RADIATION BALANCE

The radiation balance in the Spartina marsh was studied in order to have an estimation of solar energy input to at least one phase of the marsh-estuarine ecosystem.

PHYSICAL CHARACTERISTICS

To understand the dynamics of a marsh-estuarine ecosystem, the physical characteristic of the study area needs to be evaluated. The hydrography of North Inlet Estuary was described after extensive field studies. In addition, an easily accessible computer disk storage system was developed to store physical time series data for later model calibration.

SALT MARSH MICROECOSYSTEMS

The last portion of this study deals with the salt marsh microecosystems program. The initial phase was concerned with design and construction of the microecosystem marsh units. In the current phase, these units have been tested to evaluate the replicability of the several units and to compare these units with the salt marsh. The primary response studied was community metabolism. The next phase is study of the influence of specific perturbations on these experimental units.

REFERENCES

Abbott, W. Microcosm studies on estuarine waters. I. The replicability of microcosms. J. Water Pollut. Cont. Fed., 38:258-270, 1966.

Ackroyd, M. H. Digital Filters. Butterworths, London, 1973. 82 pp.

Alexander, J. E., R. Holiman, and S. A. Fisher. The oceanography of Block Island Sound. Part I - Sampling. In: Estuarine Microbial Ecology. L. H. Stevenson and R. R. Colwell, eds. University of South Carolina Press, Columbia, South Carolina, 1973. pp. 259-267.

Andersen, O. Metabolic response of the caridean shrimp Palaemonetes pugio to infection by the adult epibranchial isopod parasite Probopyrus pandalicola. Comp. Biochem. Physiol., 50A:747-775, 1975.

Bahr, L. Aspects of the structure and function of the intertidal oyster. Ph.D. Thesis, University of Georgia, Athens, Georgia, 1974. 149 pp.

Bainbridge, R. Migrations. In: The Physiology of Crustacea, Chapter 12, Vol. 2, T. H. Waterman, ed. Academic Press, New York, 1961. pp. 431-463.

Barham, E. G. Siphonophores and the deep scattering layer. Science, 140: 826-828, 1963.

_____. Deep scattering layer migration and composition: observations from a diving saucer. Science, 151:1399-1402, 1966.

Bayne, B. L. The responses of the larvae of Mytilus edulis (L.) to light and to gravity. Oikos, 15:162-174, 1964.

Beamish, P. Quantitative measurements of acoustic scattering from zooplankton organisms. Deep Sea Res., 18:811-822, 1971.

_____. The pattern of photosynthesis and respiration in laboratory microecosystems. Mem. Inst. Ital. Idrobiol., 18 suppl:61-74, 1965.

Boden, B. P. Plankton and the sonic scattering layer. Rapp. et Proc.-Verb. Val., 153:1203-1209, 1962.

_____, and E. H. Kampa. The influence of natural light on vertical migrations of an animal community in the sea. Symp. Zool. Soc. Lond., 19: 15-26, 1967.

Bosch, H. F., and W. R. Taylor. Diurnal vertical migration of an estuarine Cladoceran, Podon polyphemoides, in the Chesapeake Bay. Mar. Biol., 19: 172-181, 1973.

Brooks, J., and S. I. Dodson. Predation body size and composition of plankton. Science, 150:28-35, 1965.

Bruce, V. G., and C. S. Pittendrigh. Resetting the Euglena clock with a single light stimulus. Amer. Nat., 92:295-306, 1958.

Cadée, G. C., and J. Hegeman. Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. Neth. J. Sea Res., 8: 260-291, 1974.

Carriker, R. M. Ecological observations of the distribution of oyster larvae in New Jersey estuaries. Ecol. Monogr., 21:19-38, 1951.

_____. Ecology of estuarine benthic invertebrates: a perspective. In: Estuaries, G. H. Lauff, ed. American Association for the Advancement of Science, Washington, D. C., 1967. pp. 442-487.

Chapman, C. Channelization and spoiling in Gulf coast and south Atlantic estuaries. In: Proc. of the Marsh and Estuary Management Symp., J. D. Newsom, ed. Thos. J. Moran's Sons, Baton Rouge, Louisiana, 1968. pp. 96-107.

Cooke, G. D. The pattern of autotrophic succession in laboratory microcosms. Bioscience, 17:717-721, 1967.

Cooper, D. Responses of continuous-series estuarine microecosystems to point-source input variations. Ph.D. Thesis, University of Texas, Austin, Texas, 1970. 125 pp.

Copeland, B. J. Evidence for regulation of community metabolism in a marine ecosystem. Ecology, 46:563-564, 1965.

_____. Biological and physiological basis of indicator communities. In: Pollution and Marine Ecology, T. A. Olson and F. J. Burgess, eds. Interscience, New York, 1967. pp. 285-238.

_____, and T. C. Harris. Photosynthetic productivity in oil refinery effluent holding ponds. J. Water Pollut. Cont. Fed., 36:1104-1111, 1962.

Crisp, D. J., and D. A. Ritz. Responses of cirripede larvae to light. I. Experiments with white light. Mar. Biol., 23:327-335, 1973.

Cummings, K. W. Calorific equivalents for studies in ecological energetics. Pymatuning Laboratory, University of Pittsburgh, Pittsburg, Pennsylvania. 52 pp.

Cushing, D. H. The vertical migration of planktonic Crustacea. Biol. Rev., 26:158-192, 1951.

_____. Some experiments on the vertical migration of zooplankton. J. Animal Ecol., 24:137-166, 1955.

Daley, R. J., C. E. J. Gray, and E. H. Brown. A quantitative, semi-routine method for determining algal and sedimentary chlorophyll derivatives. J. Fish. Res. Bd. Canada, 30:345-356, 1973.

Dame, R. F. The ecological energies of growth, respiration and assimilation in the American oyster, Crassostrea virginica. Mar. Biol., 17:243-250, 1972.

_____. Energy flow in an intertidal oyster population. Estuar. and Coastal Mar. Sci., 4:243-253, 1976.

_____, and F. J. Vernberg. The influence of cyclic temperatures on the respiration of mud crabs (in preparation).

Davies, J. A. A note on the relationship between net radiation and solar radiation. Quart. J. R. Meteor. Soc., 93:109-115, 1967.

Davis, C. C. 1944. On four species of Copepods new to Chesapeake Bay with a description of a new variety of Paracalanus crassirostris Dahl. Chesapeake Biol. Lab., 61:1-11, 1944.

Day, J. W., W. G. Smith, P. R. Wagner, and W. C. Stowe. Community structure and carbon budget of a salt marsh and shallow bay estuarine system in Louisiana. Center for Wetlands Resources. Louisiana State University, Baton Rouge, Louisiana. 79 pp.

Deevey, G. B. Annual variations in length of copepods in the Sargasso Sea off Bermuda. J. Mar. Biol. Ass. U.K., 44:589-600, 1964.

Dietz, R. The seas deep scattering layers. Sci. Amer., 207:44-50, 1962.

Donaldson, H. A., and W. G. Pearcy. Sound scattering layers in the north-eastern Pacific. J. Fish. Res. Bd. Canada, 29:1419-1423, 1972.

Ekern, P. C. The fraction of sunlight retained as net radiation in Hawaii. J. Geophys. Res., 70:785-791, 1965.

Ennis, G. P. Behavioral responses to changes in hydrostatic pressure and light during larval development of the lobster Homarus gammarus. J. Fish. Res. Bd. Canada, 30:1349-1360.

Enright, J. T., and W. Hamner. Vertical diurnal migration and endogenous rhymicity. Science, 1957:937-941, 1967.

Ferguson, R. L., and M. B. Murdoch. Microbial ATP in sediments of the Newport River estuary, North Carolina. In: Estuarine Research, Vol. 1 Chemistry, Biology and the Estuarine System, L. E. Cronin, ed. Academic Press, New York.

Fleminger, A. New calanoid copepods of Pontella Dana and Labidocera Lubbock with notes on the distribution of the genera in the Gulf of Mexico. Tulane Stud. Zool., 5:19-34, 1956.

Forward, R. B., Jr. Negative phototaxis in crustacean larvae: possible functional significance. J. Exp. Mar. Biol. Ecol., 16:11-17, 1974.

Gallagher, J. L. The significance of the surface film in salt marsh plankton metabolism. Limnol. Oceanogr., 20:120-123, 1975.

Gonsález, J. G., and T. E. Bowman. Planktonic copepods from Bahía Fosforescente, Puerto Rico and adjacent waters. Proc. U.S. Natl. Mus., 117:241-304, 1965.

Grice, G. D. Calanoid and cyclopoid copepods collected from the Florida Gulf Coast and Florida Keys in 1954 and 1955. Bull. Mar. Sci. Gulf and Carib., 10:217-236, 1960.

Grindley, J. R. Effect of low salinity water on the vertical migration of estuarine plankton. Nature, 203:781-782, 1964.

Grøntved, J. On the productivity of microbenthos and phytoplankton in some Danish fjords. Meddr. Dansk. Fisk. og Havundersø. N. S., 3:55-91, 1960.

_____. Preliminary report on the productivity of microbenthos and phytoplankton in the Danish Wadden Sea. Meddr. Dansk. Fisk. og Havundersø. N. S., 3:347-372, 1962.

Hansen, D. V., and M. Rattray, Jr. New dimensions in estuary classification. Limnol. Oceanogr., 11:319-326, 1966.

Harvey, H. W. On the production of living matter in the sea off Plymouth. J. Mar. Biol. Ass. U.K., 29:97-137, 1950.

Herman, S. S. Vertical migration of the opossum shrimp, Neomysis americana Smith. Limnol. Oceanogr., 8:228-238, 1963a.

_____. Spectral sensitivity and phototaxis in the opossum shrimp, Neomysis Americana Smith. Biol. Bull., 125:563-570.

_____, J. A. Mihursky, and A. J. McErlean. Zooplankton and environmental characteristics of the Patuxent River Estuary, 1963-1965. Chesapeake Sci., 9:67-82, 1968.

Herrnkind, W. F. The brooding of Uca pugilator and mass rearing of the larvae with comments on the behavior of the larval and early crab stages. Crustaceana, Suppl. 3:215-234, 1968.

Holland, A. F. The biology and ecology of Tagelus plebeius. M.S. Thesis, University of South Carolina, Columbia, South Carolina, 1973. 96 pp.

_____, and J. H. Dean. The community biology of intertidal macrofauna inhabiting sandbars in the North Inlet area of S. C. In: Ecology of Marine Benthos, B. C. Coull, ed. University of South Carolina Press, Columbia, South Carolina (in press).

Holm-Hansen, V., and C. R. Booth. The measurement of adenosine triphosphate in the ocean and its ecological significance. Limnol. Oceanogr., 11: 510-519, 1966.

Hughes, D. A. On the endogenous control of tide-associated displacements of pink shrimp, Penaeus duorarum Burkenroad. Biol. Bull., 143:371-380, 1972.

Hughes, R. N. An energy budget for a tidal-flat population of the bivalve Scrobicularia plana (DaCosta). J. Anim. Ecol., 39:357-380, 1970.

Hunding, C. Production of benthic microalgae in the littoral zone of a eutrophic lake. Oikos, 22:389-397, 1971.

Hunt, J. N. Tidal oscillations in estuaries. Geophys. J. Roy. Astro. Soc., 8:440-455, 1964.

Isaacs, J. D., R. A. Tont, and G. L. Wick. Deep scattering layers: vertical migration as a tactic for food finding. Deep-Sea Res., 21:651-656.

Jeffries, H. P. Succession of two Acartia species in estuaries. Limnol. Oceanogr., 7:354-364, 1962.

Johnson, R. G. Variations in diversity within benthic marine community. Amer. Nat., 104:285-300, 1970.

Kampa, E. M. Photoenvironment and sonic scattering. In: Proceedings of an International Symposium on Biological Sound Scattering in the Ocean, B. Farquhar, ed. Maury Center for Ocean Science, Washington, D. C., 1971. pp. 51-58.

_____. Photoenvironment and vertical migrations of mesopelagic marine animal communities. In: Biological Rhythms in the Marine Environment, P. DeCoursey, ed. University of South Carolina Press, Columbia, South Carolina, 1976. pp. 257-272.

Kevern, N. R., and R. C. Ball. Primary productivity and energy relationships in artificial streams. Limnol. Oceanogr., 10:74-87, 1965.

Kjerfve, B. Velocity averaging in estuaries characterized by a large tidal range to depth ratio. Estuar. and Coastal Mar. Sci., 3:311-323, 1975.

———, and H. S. Ivester. Reversal of the net flow in a Georgia estuary. Abstract. Trans. Am. Geophys. U., 55:1136. Paper presented at the fall meeting of the AGU in San Francisco, California, 1974.

———, ———, and D. J. Lonsdale. Circulation of the North Inlet Estuary. Abstract. Am. Soc. Limnol. Oceanogr. 18th annual meeting, Halifax, N.S., 1975.

Krumbein, W. E. Sediment microbiology and grain-size distribution, as related to tidal movement, during the first mission of the West German Underwater Laboratory "Helgoland." Mar. Biol., 10:101-112, 1971.

Muenster, E. S. Structure and energy flow of a mussel population in a Georgia salt marsh. Limnol. Oceanogr., 6:191-204, 1961.

Lance, J. Effect of reduced salinity on the vertical migration of zooplankton. J. Mar. Biol. Ass. U.K., 42:131-153, 1962.

Lauff, G. H. Introduction. In: Estuaries, G. H. Lauff, ed. American Association for the Advancement of Science, Publ. No. 83. pp. v-vi.

———, and K. W. Cummings. A model stream for studies in lotic ecology. Ecology, 45:188-190, 1964.

Leach, J. H. Epibenthic algal production in an intertidal mudflat. Limnol. Oceanogr., 15:514-521, 1970.

———. Hydrology of the Ythan Estuary with reference to distribution of major nutrients and detritus. J. Mar. Biol. Ass. U.K., 51:137-157, 1971.

Lincoln, R. J. A lab investigation of effects of hydrostatic pressure on vertical migration of planktonic crustacea. Mar. Biol., 6:5-11, 1970.

———. Observations on effects of changes of hydrostatic pressure and illumination on behavior of planktonic crustacea. J. Exp. Biol., 54: 677-688, 1971.

Maly, E. J., and M. P. Maly. Dietary differences between two co-occurring calanoid copepod species. Oecologia, 17:129-133, 1974.

Marshall, N., C. A. Oviatt, and D. M. Skauen. Productivity of the benthic microflora of shoal estuarine environments in southern New England. Int. Revue ges. Hydrobiol., 56:947-955, 1971.

McHugh, J. L. Estuarine nekton. In: Estuaries, G. H. Lauff, ed. American Association for the Advancement of Science, Publ. No. 83, 1967. pp. 581-620.

McIntire, C. D., R. L. Garrison, H. K. Phinney, and C. E. Warren. Primary production in laboratory streams. Limnol. Oceanogr., 9:92-102, 1964.

McLaren, I. A. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Bd. Can., 20: 685-727, 1963.

McNeil, S., and J. H. Lawton. Annual production and respiration in animal populations. Nature, 225:472-474, 1970.

Miller, C. B. Some environmental consequences of vertical migration in marine zooplankton. Limnol. Oceanogr., 11:727-741, 1970.

Monteith, J. L., and G. Szeicz. The radiation of bare soil and vegetation. Quart. J. R. Meteor. Soc., 87:159-170, 1961.

_____, and _____. Radiative temperature in the heat balance of natural surfaces. Quart. J. R. Meteor. Soc., 88:496-507, 1962.

Morita, R. Y., L. P. Jones, P. Griffiths, and T. E. Staley. Salinity and temperature interactions and their relationship to the microbiology of the estuarine environment. In: Estuarine Microbial Ecology, L. H. Stevenson and R. R. Colwell, eds. University of South Carolina Press, Columbia, South Carolina, 1973. pp. 221-232.

Muhlstaff, H. J., and M. H. Reeves. Analysis of linear compartment models for ecosystems. J. Theor. Biol., 44:105-116, 1974.

Nixon, S. W., and C. A. Oviatt. Ecology of a New England salt marsh. Ecol. Monogr., 43:463-498, 1973.

Odum, H. T. Environment, Power and Society. Wiley-Interscience, New York. 331 pp.

_____, and A. Chestnut. Estuarine microecosystems receiving sewage. Sea Grant Report, University of North Carolina, Chapel Hill, North Carolina, 1970. 83 pp.

_____, and A. de la Cruz. Particulate organic detritus in a Georgia salt marsh-estuarine ecosystem. In: Estuaries, G. H. Lauff, ed. American Association for the Advancement of Science, Publ. No. 83, 1967. pp. 383-388.

_____, C. M. Hoskin. Metabolism of a laboratory stream microcosm. Publ. Inst. Mar. Sci., Univ. Texas, 4:115-133, 1957.

_____, and A. E. Smalley. Comparison of population energy flow of a herbivorous and a deposit-feeding invertebrate in a salt marsh ecosystem. Proc. Natl. Acad. Sci., 45:617-622, 1959.

_____, E. J. Copeland, and E. A. McMahan. Coastal Ecological Systems of the United States, 4 volumes. The Conservation Foundation, Washington, D. C., 1974.

Palmer, R. D. Biological Clocks in Marine Organisms. John Wiley and Sons, 1974. 173 pp.

Pamatmat, M. M. Ecology and metabolism of a benthic community on an intertidal sand flat. Int. Revue ges. Hydro. Biol., 53:211-298, 1968.

Patten, B. C. Systems Analysis and Simulation in Ecology, Vol. 1. Academic Press, New York. 607 pp.

_____. Systems Analysis and Simulation in Ecology, Vol. 2. Academic Press, New York. 592 pp.

_____. Ecosystem linearization: an evolutionary design problem. In: Ecosystem Analysis and Prediction, S. Levin, ed. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania, 1975. 137 pp.

Pearre, S., Jr. Vertical migration and feeding in Sagitta elegans Verrill. Ecology, 54:300-314, 1973.

Petersen, C. G. Valuation of the sea. II. The animal communities of the sea bottom and their importance for marine zoogeography. Danish. Biol. Stat. Copenhagen, Rep. 21, 1913. 68 pp.

Pinschmidt, W. D., Jr. Distribution of crab larvae in relation to some environmental conditions in the Newport River estuary, North Carolina. Ph.D. Thesis, Duke University, Durham, North Carolina, 1963. 113 pp.

Polavarapu, R. J. A comparative study of global and net radiation measurements at Guelph, Ottawa and Toronto. J. Appl. Meteor., 9:609-614, 1970.

Pomeroy, L. R. Algal productivity in salt marshes of Georgia. Limnol. Oceanogr., 4:386-397, 1959.

Pritchard, D. W. Estuarine circulation patterns. Proc. Am. Soc. Civil Engr., 81:717/1-717/11.

Ragotzkie, R. A. Plankton productivity in estuarine waters of Georgia. Publ. Inst. Mar. Sci., Univ. Texas, 5:146-158, 1959.

Reeve, M. R. Seasonal changes in the zooplankton of South Biscayne Bay and some problems of assessing the effects on the zooplankton of natural and artificial thermal and other fluctuations. Bull. Mar. Sci., 20: 894-921, 1970.

Riley, G. A. Plankton studies. III. Long Island Sound. Bull. Bingh. Oceanogr. Coll., 7:1-93, 1941.

_____. Oceanography of Long Island Sound. Bull. Bingh. Oceanogr. Coll., 15:324-344, 1956.

Ringelberg, J. The positively phototactic reaction of Daphnia magna Straus: A contribution to the understanding of diurnal vertical migration. Neth. J. Sea Res., 2:319-406, 1964.

Rudjakov, J. A. The possible causes of diel vertical migration of planktonic animals. Mar. Biol., 8:98-105.

_____, and N. N. Voronina. Diurnal vertical migration of Metridia seriechai in the Scotia Sea. Oceanologia, 13:513-514, 1973. (Summary in English)

Ryther, J. H. Geographic variations in productivity. In: The Sea, Vol. 2, M. N. Hill, ed. Interscience, New York, 1963. pp. 347-380.

Sage, L. E., and S. S. Herman. Zooplankton of the Sandy Hook Bay area, N. J. Chesapeake Sci., 13:29-39, 1972.

Sameoto, D. D. Tidal and diurnal effects on zooplankton sample variability in a nearshore marine environment. J. Fish. Res. Bd. Can., 32:347-355, 1975.

Sandifer, P. A. The distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay, Virginia, 1968-1969. Chesapeake Sci., 14:235-257, 1973.

Schelske, C. L., and E. P. Odum. Mechanisms maintaining high productivity in Georgia estuaries. Gulf Caribb. Fish. Inst. Proc., 14:75-80, 1961.

Schmidt, R. A. Needed - A coastline comprehensive program for the development of estuaries. In: Symp. on Estuarine Fisheries, Amer. Fish. Soc. Spec. Publ. 3, 1966. pp. 103-109.

Selmer, R. Survival and metabolism of the harpacticoid Thompsonula hyaenae fed on different diatoms. Hydrobiological (in press).

Selmer, R. G. Primary production and the release of dissolved organic matter from natural communities of estuarine phytoplankton. M.S. Thesis, University of South Carolina, Columbia, South Carolina, 1973. 45 pp.

_____, R. G. Zingmark, and T. G. Miller. Interpretations of the ^{14}C method of measuring the total annual production of phytoplankton in a South Carolina estuary. Bot. Mar., 19:119-135, 1976.

Simms, J. Vaucheria compacta: A euryhaline estuarine algal species. Acta Bot. Neerl., 23:613-626, 1974.

Smalley, A. E. The growth cycle of Spartina and its relation to the insect populations in the marsh. Proc. Salt Marsh Conf., Sapelo Island, Georgia, 1959. pp. 101-107.

Stanhill, G., G. J. Hofstede, and J. D. Kalma. Radiation balance of natural and agricultural vegetation. Quart. J. R. Meteor. Soc., 92:128-140, 1966.

McCrone, J. H., and I. E. Baird. Production ecology of sandy beach. Limnol. Oceanogr., 13:16-23, 1968.

Steeman-Nielsen, E. A survey of recent Danish measurements of the organic productivity in the sea. Rapp. Cons. Explor. Mer., 144:92-95, 1958.

Stevenson, L. H., C. E. Hillwood, and B. H. Gebeler. Aerobic, heterotrophic bacterial populations in estuarine water and sediments. In: Effect of the Ocean Environment on Microbial Activities, R. R. Colwell and R. Y. Morita, eds. University Park Press, Baltimore, Maryland, 1974. pp. 268-285.

Strome, R. G., and J. R. Stottlemyer. Primary production in the Patuxent River. Chesapeake Sci., 6:125-140, 1965.

Sulkin, S. Influence of light in the depth regulation of crab larvae. Biol. Bull., 148:333-343, 1975.

Sutcliffe, W. H., Jr. A list of calanoid copepods from the plankton at Beaufort, N. C. J. Elisha Mitchell Scient. Soc., 64:234-236, 1948.

Taylor, W. R. Marine Algae of the Northeastern Coast of North America, Second Revised Edition. University of Michigan Press, Ann Arbor, Michigan. 509 pp.

Teal, J. M. Energy flow in the saltmarsh ecosystem of Georgia. Ecology, 43: 614-624, 1962.

Tenore, K. R., and W. M. Dunstan. Comparison of feeding and biodeposition of three bivalves at different food levels. Mar. Biol., 21:190-195, 1973.

Thayer, G. W. Phytoplankton production and the distribution of nutrients in a shallow unstratified estuarine system near Beaufort, N. C. Chesapeake Sci., 12:240-253, 1971.

_____, H. Adams, and M. W. LaCroix. Structural and functional aspects of a recently established Zostera marina community. Estuar. Res., 1:518-540, 1975.

_____, D. A. Wolf, and R. B. Williams. The impact of man on seagrass systems. Am. Sci., 63:288-296, 1975.

_____, D. E. Hoss, M. A. Nielsen, W. F. Hettler, Jr., and M. W. LaCroix. Biomass of zooplankton in the Newport River Estuary and the influence of post larval fishes. Chesapeake Sci., 15:9-16, 1974.

Thomas, J. P. Influence of the Altamaha River on primary production beyond the mouth of the river. M.S. Thesis, University of Georgia, Athens, Georgia, 1966. 46 pp.

Thorson, G. Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. Ophelia, 1:167-208, 1964.

Valiela, I., G. Vince, and J. M. Teal. Assimilation of sewage by wetlands. Adv. Estuar. Res. (in press).

Vatova, A. Primary production in the High Venice Lagoon. J. Cons. Int. Explor. Mer., 28:148-155, 1963.

Vernberg, F. J. Acclimation of intertidal crabs. Am. Zool., 9:113-141, 1969.

Vernberg, W. B. Metabolic-environmental interaction in marine plankton. In: Fifth European Marine Biology Symposium, B. Battaglia, ed. Piccin Editore, Padua, 1972. pp. 189-196.

_____, and B. C. Coull. Respiration of an interstitial ciliate and benthic energy relationships. Oecologia, 16:259-264, 1974.

_____, F. J. DeCoursey, and W. Padgett. Synergistic effects of environmental variables on larvae of Uca pugilator. Mar. Biol., 22:307-312, 1973.

Verwey, J. The role of some external factors in the vertical migration of marine animals. Neth. J. Sea Res., 3:249-266, 1966.

Walsh, G. E. An ecological study of a Hawaiian mangrove swamp. In: Estuaries, G. H. Lauff, ed. American Association for the Advancement of Science, Publ. No. 83, 1967. pp. 420-431.

Weiss, W. B., and T. L. Hopkins. The zooplankton of the Anclote River Estuary, Florida. Abstract. Am. Soc. Limnol. Oceanogr. 18th Meeting, Halifax, N. S., 1975. 67 pp.

Whittaker, R. H. Experiments with radiophosphorus tracer in aquarium microcosms. Ecol. Monogr., 31:157-188, 1961.

Wiegert, R. G. Mathematical representation of ecological interactions. In: Ecosystem, Analysis and Prediction, S. Levin, ed. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania. 337 pp.

_____, R. R. Christian, J. L. Gallagher, J. R. Hall, R. D. H. Jones, and R. L. Wetzel. A preliminary model of a coastal Georgia Spartina marsh. Estuar. Res., 1:383-661, 1975.

Wilhm, J. L., and J. Lang. Succession in algal mat communities at three different nutrient levels. Ecology, 50:645-652, 1969.

Williams, R. B. Annual phytoplanktonic production in a system of shallow temperate estuaries. In: Some Contemporary Studies in Marine Science, H. Barnes, ed. Lang: George Allen and Unwin Ltd., London, 1966. pp. 699-716.